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CONTENTS OF VOLUME 13

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Five Natural Hybrid Combinations in Minnows (Cyprinidae)

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The hybrid fishes described herein are *Chrosomus erythrogaster* (Rafinesque) × *Notropis cornutus frontalis* (Agassiz), *C. erythrogaster* × *Semotilus atromaculatus* (Mitchill), *Campostoma anomalum plumbeum* (Girard) × *S. atromaculatus, Gila nigrescens* (Girard) × *Rhinichthys cataractae* (Valenciennes), and *Notropis venustus venustus* (Girard) × *Notropis whipplei* (Girard). Two of the combinations have been reported, without descriptions, in literature (citations below), and Hubbs (1955: Fig. 3) graphically indicated hybridization between the same genera with which this paper is concerned, but did not designate the species involved.

All specimens of *C. erythogaster* × *N. c. frontalis, C. erythrogaster* × *S. atromaculatus, C. a. plumbeum* × *S. atromaculatus,* and *N. v. venustus* × *N. whipplei* were taken in a period of severe drought in Kansas and Arkansas. All were from small, spring-fed streams that support large populations of fishes. That the drought of 1953-1956 had pronounced effects on stream habitats in Kansas has been documented by Minckley and Cross (1959). Satisfactory sites for spawning may have been few, but an abundance of adult fishes persisted from earlier, wet years. Unusual crowding of spawning fishes would increase the opportunity for fertilization of the eggs of one species by sperm from another species. We think that the hybrids reported here (excepting *G. nigrescens* × *R. cataractae*) are explainable on the basis of crowding; we have no information about stream-conditions where the last-named hybrid was found. Generally, hybridization of fishes seems most common in areas that have been subject to radical climatic change in the past 20,000 or fewer years (Hubbs, 1955: 18-19), and in streams that have been altered recently by the activities of man (Hubbs and Strawn, 1956:342, and others). Streams from which we report hybrids probably were affected by overgrazing of their watersheds; overgrazing was unusually severe in the drought.

Most of the hybrids were recognized as unusual at the time of capture, and were saved as part of numerically selective samples from the streams (rather than being discovered in the laboratory, in random samples).

Our measurements were made by methods defined by Hubbs and Lagler (1958); values are expressed as thousandths of the larger dimension.

***Chrosomus erythrogaster* × *Notropis cornutus frontalis*:** KU 3872 (26.7 mm. in standard length) and KU 4170 (46.6 mm.) from Deep Creek, Riley Co., Kansas, Sec. 23, T. 11S, R. 7E, Dec. 14, 1957, and Apr. 26, 1958, respectively; and KU 4185 (39.3 mm.) from Bluff Creek, Pottawatomie Co., Kansas, Sec. 15, T. 6S, R. 8E, June 29, 1958. Compared in Table 1 with five specimens of *C. erythrogaster,* KU 3914 (39.3 to 47.3 mm., mean 43.0 mm.) from the same locality and of the same date as KU 3872 (above); and with five specimens of *N. c. frontalis,* KU 4184 (41.0 to 46.5 mm., mean 42.5 mm.) from the same locality and of the same date as KU 4185 (above). This cross has previously been recorded by Trautman (1957:326, 355) and by Minckley (1959:431).

The head-lengths of the hybrids are greater than in specimens of like size of *C. erythrogaster* or *N. c. frontalis* (Table 1). Hubbs and Miller (1943:373-374) reported that hybrids of *Gila orcutti* × *Siphateles mohavensis* have larger, more robust heads than either of the parental species, perhaps because of heterosis. The enlarged heads in hybrids of *C. erythrogaster* and *N. c. frontalis* result primarily from elongation of the postorbital region, with lesser elongation of the snout and orbit. The enlarged head affects measurements obtained for other structures that are parts of the head (and expressed as proportions of standard length or head-length), causing a tendency toward *N. c. frontalis* when the head-part is divided by standard length, and greater intermediacy or a tendency toward *C. erythrogaster* when the head-part is divided by head-length. In characters in which the parental species differ most (size of eye, length of upper jaw, and width of gape), the hybrids are intermediate between the parental species, regardless of whether the measurements are expressed as proportions of head-length or standard length; however, tendencies toward one or the other of the parental species (dependent on the divisor) can also been seen in these characters. Some experimentally propagated hybrids show highly variable, and sometimes extreme characters, rather than intermediacy of meristic and proportional characters (Hubbs, 1956).

Table 1. Comparisons of Three Specimens of Chrosomus erythrogaster × Notropis cornutus frontalis with Specimens of the Parental Species (means are above, ranges in parentheses below)

	Chrosomus erythrogaster	KU 4170 and 4185	KU 3872	*Notropis c. frontalis*
Standard lengths	43.0 (39.3–47.3)	43.0 (39.3–46.6)	26.7	42.5 (41.0–46.5)
$\frac{\text{Head-length}}{\text{Standard length}}$	253 (246–262)	282 (280–283)	307	276 (273–283)
$\frac{\text{Orbital length}}{\text{Standard length}}$	067 (063–071)	075 (071–079)	101	083 (080–086)
$\frac{\text{Orbital length}}{\text{Head-length}}$	263 (252–272)	266 (250–282)	329	300 (291–310)
$\frac{\text{Snout-length}}{\text{Standard length}}$	069 (068–071)	073 (071–075)	071	068 (066–071)
$\frac{\text{Snout-length}}{\text{Head-length}}$	272 (262–280)	260 (255–265)	232	245 (233–260)
$\frac{\text{Interorbital width}}{\text{Standard length}}$	069 (065–071)	074 (069–079)	079	068 (067–069)
$\frac{\text{Interorbital width}}{\text{Head-length}}$	272 (262–286)	263 (245–280)	256	245 (241–250)
$\frac{\text{Gape-width}}{\text{Standard length}}$	056 (051–059)	065 (059–071)	064	065 (062–066)
$\frac{\text{Gape-width}}{\text{Head-length}}$	222 (204–241)	230 (209–250)	207	233 (224–239)
$\frac{\text{Upper jaw-length}}{\text{Standard length}}$	057 (051–061)	082 (076–088)	112	083 (080–086)
$\frac{\text{Upper jaw-length}}{\text{Head-length}}$	223 (206–237)	292 (273–311)	268	301 (284–315)
$\frac{\text{Postorbital length}}{\text{Standard length}}$	113 (108–120)	130 (129–130)	124	123 (121–125)
$\frac{\text{Postorbital length}}{\text{Head-length}}$	444 (432–456)	460 (455–464)	402	446 (431–457)

TABLE 1. COMPARISONS OF THREE SPECIMENS OF CHROSOMUS ERYTHROGASTER × NOTROPIS CORNUTUS FRONTALIS WITH SPECIMENS OF THE PARENTAL SPECIES (MEANS ARE ABOVE, RANGES IN PARENTHESES BELOW)—*Concluded*

	Chrosomus erythrogaster	KU 4170 and 4185	KU 3872	*Notropis c. frontalis*
Length of depressed dorsal fin / Standard length	224 (217–232)	250 (247–252)	255	237 (233–243)
Length of depressed dorsal fin / Head-length	885 (869–892)	886 (871–900)	829	858 (836–890)
Number scales in lateral line	71.7 (68–76)	53.0 (53.0)	52(?)	38.8 (38–39)
Pharyngeal teeth	0,5–5,0	1,5–4,1 ((?)–4,1)	1,5–4,2	2,4–4,2
Anal rays	8	8	8	usually 9
Vertebrae	37–40	39	....	38–39

In pigmentation, all three of the hybrids are intermediate between the parental species. The mid-lateral band (which is dark and discrete in *C. erythrogaster,* but faint, broad, and diffuse in *N. c. frontalis*) is broader and fainter in the hybrids than in *Chrosomus,* but is better developed than in *N. c. frontalis.* The dorsolateral dark band of *C. erythrogaster* is present in the hybrids, but is less distinct than in that species, and less distinct than the mid-lateral band of the hybrids themselves. The dorsolateral band is not present in *N. c. frontalis.* The color of the peritoneum in the hybrids is the glossy, jet-black of *C. erythrogaster* in two specimens, and the dusky-black of *N. c. frontalis* in one.

Chrosomus and *Notropis* differ greatly in the length and convolution of the intestine. *Chrosomus* has a long, coiled gut, which is crossed by the mid-ventral line eight or nine times; in *N. c. frontalis,* the intestine forms a flat, S-shaped loop that does not cross the mid-ventral line. In the two largest hybrids (KU 4170 and 4185), the gut is intermediate, crossing the mid-ventral line four times. In the smaller hybrid (KU 3872) the gut crosses the mid-ventral line twice but the configuration of the anterior loops indicates that the same intestinal convolutions that were found in the larger specimens would have developed in KU 3872 as the gut elongated with increase in size of the fish.

Both Deep and Bluff creeks are clear, gravel-bottomed streams draining parts of the Flint Hills Area of Kansas. A description of Flint Hills streams and lists of fishes occurring in them have been published by Minckley (1956 and 1959), and by Minckley and Cross (1959).

Chrosomus erythrogaster × *Semotilus atromaculatus:* KU 2947 (28.0 mm. in standard length) from Mill Creek, Wabaunsee Co., Kansas, Sec. 30, T. 12S, R. 9E, Mar. 22, 1953. Compared in Table 2 with five specimens of *C. erythrogaster,* KU 2836 (27.2 to 31.0 mm., mean 28.5) from the same locality and of the same date as KU 2947 (above); and with five specimens of S. *atromaculatus,* KU 1954, 2499, 2703, and 2838 (25.5 to 31.1 mm., mean 28.9 mm.) from streams in the same area.

This hybrid is intermediate between the two species in number of scales and pharyngeal teeth, and has a composite of the pigmentation found in the parental fishes (Table 2). For diagnostic purposes, greater importance is attached to the characters mentioned above than to proportional measurements, which are subject to considerable error because of the small size of the specimens. The few measurements that were taken indicate that this hybrid, like *C. erythrogaster* × *N. c. frontalis,* has a larger head than do specimens of like size of either parental species. The enlarged head affects measurements obtained for other structures that are parts of the head; only the length of the upper jaw, which is greatly different in the parental species, is actually intermediate in KU 2947.

Mill Creek is a clear stream, similar to Deep and Bluff creeks but somewhat larger. Mill Creek had an exceptionally large population of fishes at the time the hybrid was found, but *Chrosomus* and *Semotilus* were neither unusually common nor rare.

Two other crosses, both of which have been described in the literature, also have been found in Mill Creek. These are *N. c. frontalis* × S. *atromaculatus,* and *N. c. frontalis* × *Notropis rubellus* (Agassiz).

***Campostoma anomalum plumbeum* × *Semotilus atromaculatus*:** KU 4013 (three males, 86.0 to 96.0 mm. in standard length, mean 89.5 mm.) from Timber Creek, Scott Co., Kansas, Sec. 2, T. 16S,

Table 2. Comparison of One Specimen of Chrosomus erythrogaster × Semotilus atromaculatus with Specimens of the Parental Species (means are above, ranges in parentheses below)

	Chrosomus erythrogaster	KU 2947	*Semotilus atromaculatus*
Dark lateral band	intense	intense	intense
Light dorsolateral band	well-defined	poorly developed	absent
Dark dorsolateral band	intense	poorly developed	absent
Color of peritoneum	black	black	silvery
Length of gut	long with transverse coils	short, with a single forward loop	short, with a single forward loop
Pharyngeal teeth	0,5–5,0	1,5–5,2	usually 2,5–4,2
Number scales in lateral line	usually 70 or more, embedded	about 67 slightly embedded	usually fewer than 65, not embedded
Barbels	absent	absent	usually present
Vertebrae	37–40	39	42–43
$\frac{\text{Head-length}}{\text{Standard length}}$	272 (266–277)	310	300 (292–308)
$\frac{\text{Upper jaw-length}}{\text{Standard length}}$	071 (069–074)	097	110 (104–114)
$\frac{\text{Upper jaw-length}}{\text{Head-length}}$	263 (254–273)	310	366 (356–382)
$\frac{\text{Interorbital width}}{\text{Standard length}}$	103 (101–106)	114	116 (114–118)
$\frac{\text{Interorbital width}}{\text{Head-length}}$	381 (372–400)	372	388 (380–400)
$\frac{\text{Orbital length}}{\text{Standard length}}$	081 (075–085)	083	078 (076–084)
$\frac{\text{Orbital length}}{\text{Head-length}}$	296 (271–313)	267	261 (255–273)

R. 33W, June 19, 1958. Compared in Table 3 with five specimens of *C. a. plumbeum*, KU 4034 (85.7 to 93.1 mm., mean 90.2 mm.) from the Smoky Hill River, Wallace Co., Kansas, Sec. 26, T. 13S, R. 39W, June 20, 1958; and with five specimens of *S. atromaculatus*,

TABLE 3. COMPARISONS OF THREE SPECIMENS OF CAMPOSTOMA ANOMALUM PLUMBEUM × SEMOTILUS ATROMACULATUS WITH SPECIMENS OF THE PARENTAL SPECIES (MEANS ARE ABOVE, RANGES IN PARENTHESES BELOW)

	Campostoma a. plumbeum	KU 4013 (three spec.)	*Semotilus atromaculatus*
Standard lengths	90.2 (85.7–93.1)	89.5 (85.7–96.2)	91.7 (85.0–97.5)
$\frac{\text{Predorsal length}}{\text{Standard length}}$	511 (505–517)	533 (523–542)	557 (547–564)
$\frac{\text{Head-length}}{\text{Standard length}}$	251 (244–258)	276 (273–278)	289 (280–299)
$\frac{\text{Snout-length}}{\text{Standard length}}$	090 (086–096)	088 (087–091)	085 (082–087)
$\frac{\text{Orbital length}}{\text{Standard length}}$	044 (043–045)	048 (047–049)	049 (048–050)
$\frac{\text{Interorbital width}}{\text{Standard length}}$	075 (073–078)	094 (091–099)	110 (104–113)
$\frac{\text{Distance from tip of mandible to tip of maxillary}}{\text{Standard length}}$	057 (053–063)	076 (072–078)	098 (095–104)
Gill rakers (1st arch)	30 (29–31)	17 (16–18)	9 (8–10)
Number scales in lateral line	54 (53–55)	54 (54–55)	56 (52–64)
Predorsal scale-rows	25 (23–27)	27 (27–28)	35 (34–36)
Anal rays	7 (6–7)	7.3 (7–8)	8 8
Vertebrae	40	42–44*	42–43

* Three deformed vertebrae in one specimen with 44; other two specimens have 42 vertebrae.

KU 4012 and 4047 (85.0 to 97.5 mm., mean 91.7 mm.) from the same locality and of the same date as KU 4013 (above), and Sappa Creek, Decatur Co., Kansas, Sec. 29, T. 2S, R. 28W, June 23, 1958, respectively. This hybrid combination has previously been recorded by Johnson (1945).

The hybrids seem uniformly intermediate between the parental species. Application of the hybrid index to the characters listed in Table 3 results in a value of 55.7 when *C. a. plumbeum* is assigned the value 0.

The pharyngeal arches of the hybrids are peculiarly deformed. Expressed in terms of the one- or two-rowed arrangement common to all North American cyprinids, tooth-counts of 0,5-4,1; 1,3(?)-4,0; and 2,5-4,1 best fit the three fish. However, one arch bears only three teeth, all deformed and badly aligned, plus a pit that presumably represents a lost fourth tooth. At the other extreme, one arch bears eight teeth, some of which are attached to the arch between and behind others that are countable as part of the basic main row. Supernumerary teeth and other deformities may have resulted from abnormalities in the replacement process. In some cases, replacement teeth probably failed to develop; in others, replacement teeth seemingly developed, but attached to the arch in abnormal positions, with or without loss of previous teeth, causing irregularity in alignment. Hubbs (1951) described an irregular (seemingly three-rowed) alignment in a fish that Hay (1888:249) reported from western Kansas as *Squalius elongatus*. However, Hubbs considered the specimen to be an aberrant example of *S. atromaculatus*, and the characteristics that he lists for it do not correspond closely with those of the hybrid specimens that we have. Evans and Deubler (1955:32) found three rows of teeth in two of 150 specimens of *Semotilus*, and attributed the abnormality to failure of old teeth to fall out after formation of new teeth. The teeth of *Campostoma* usually number 0,4-4,0, and those of *Semotilus* 2,5-4,2. The pharyngeal arches are much smaller in *Campostoma* than in *Semotilus*.

The peritoneum is mottled dark and silvery in the hybrids; it has a composite of the coloration in the parental species rather than a blended shade. The intestine has two diagonal loops crossing the ventral part of the body cavity, and the hindgut lies high in the cavity, along the left side of the air bladder. In *Campostoma*, the long gut is transversely coiled around the air bladder, whereas in *Semotilus* the gut forms a longitudinal, flattened, S-shaped loop, ventral to the air bladder.

In the hybrids, the mouth is slightly oblique and nearly terminal. The lower lip is thick and fleshy, but has only a suggestion of the projecting mandibular shelf that is unique in *Campostoma.* The upper lip is uniform in width, not medially expanded as in *S. atromaculatus.* One of the hybrids lacks barbels, one has a *Semotilus*-like barbel on the right side only, and one has a vestigial barbel on the right side and an anomalous barbel that is nearly terminal on the left upper lip.

In coloration, the hybrids lack the spot in the anterior base of the dorsal fin that is characteristic of *Semotilus,* but each has a poorly-developed dark lateral band, and a weak basicaudal spot. This band and spot are usually prominently developed in *S. atromaculatus* and usually are absent in adults of *C. a. plumbeum.*

In the position and obliquity of the mouth, basic color pattern (diffuse lateral band and basicaudal spot), and the presence in one specimen of a nearly terminal, barbel-like structure, the hybrids somewhat resemble *Hybopsis biguttata* (Kirtland), which occurs rarely in the Kansas River Basin. These partial similarities are coincidental, because other characters of the hybrids make relationship with *H. biguttata* implausible. The high number of gill rakers (Table 3) and the length and position of the gut indicate strongly that the three specimens are hybrids with *C. anomalum* as one parent; the pharyngeal arches, though deformed, indicate that the other parental species has two rows of teeth, with five teeth in the main row. Only *S. atromaculatus*, among species in the Kansas River Basin, usually has such a dental formula, and other characters of our three specimens fit expectations in a hybrid between that species and *C. a. plumbeum.*

Timber Creek, where the three hybrids were collected, is a small, spring-fed, sandy-bottomed tributary to Scott County State Lake in the extreme southwestern part of the Kansas River Basin. The stream was less than 10 feet wide and six inches deep, except in three pools near road crossings. The hybrids were found in two of these pools, along with numerous *S. atromaculatus* and one adult *C. a. plumbeum.*

Another specimen of *C. a. plumbeum* × *S. atromaculatus* (KU 4841, 39.3 mm. in standard length) was taken in the North Platte River at Lisco, Garden County, Nebraska, on September 11, 1959. That specimen has 7 anal rays and 52 scales in the lateral line; otherwise, it is similar to the three hybrids described above.

Gila nigrescens × *Rhinichthys cataractae:* KU 4253 (a male, 60.6 mm. in standard length), from New Mexico, Bernalillo County, Rio Grande 12 mi. S Bernalillo on U. S. Highway 85 (Corraleo Bridge). Compared in Table 4 with six specimens of *G. nigrescens:* KU 4251, 4254, and 4262 (63.1-72.4 mm. in standard length, mean 66.4 mm.); and with five specimens of *R. cataractae:* KU 4248, 4258, and 4264 (55.6-65.0 mm. standard length, mean 59.5 mm.). Comparative material was taken at the same locality as KU 4253 and at nearby localities in the Rio Grande.

The hybrid is intermediate in almost all of the features in which the parental species differ from each other. For six of the characters included in Table 4, the hybrid index is 49.7 per cent, when *Gila* is assigned the value 0 (height of dorsal fin and numbers of fin rays and teeth excluded). There is no enlargement of the head in KU 4253, such as was found in *Gila orcutti* × *Siphateles mohavensis* (Hubbs and Miller, 1943:373), *Chrosomus erythrogaster* × *Notropis cornutus frontalis,* and *C. erythrogaster* × *Semotilus atromaculatus.* The height of the dorsal fin, which Hubbs and Miller (*loc. cit.*) found to be extreme in *G. orcutti* × *S. mohavensis,* exceeds the average for the parental species in *G. nigrescens* × *R. cataractae* also; but, dorsal fins as high as that of the hybrid were found in some individuals of both parental species. In *R. cataractae,* all fins are more rounded and more expansive than in *G. nigrescens,* and fins other than the dorsal have an intermediate size in the hybrid. This intermediacy has doubtful significance, because fin-size in *Rhinichthys* varies greatly with body-size, sex, and probably with the state of sexual development. *Rhinichthys* matures at smaller size than *Gila,* and never becomes so large as that species.

Gila nigrescens and *R. cataractae* differ strikingly in features involving the snout and mouth, and these differences provide the most conclusive evidence that KU 4253 is a hybrid of these species. The projecting, fleshy snout of *R. cataractae* is bridged to the ventral mouth by a frenum that is approximately 3 mm. wide in specimens 60 mm. in standard length. In *Gila,* the snout does not project beyond the mouth, which is oblique, lacks a frenum, and is larger than in *Rhinichthys.* The snout of the hybrid projects less than in *R. cataractae* and is bridged to the upper lip by a frenum 1.7 mm. wide. The mouth of the hybrid is intermediate in size, obliquity, and thickness of the lips. *Rhinichthys* has barbels, *Gila* lacks them, and the hybrid has one vestigial barbel, on the right side. The lower surface of the head of *Rhinichthys* is broad and flattened, with pronounced rugosity on the gular area and isthmus. In *Gila* the underside of the head is convex, with comparatively smooth membranes; the hybrid is intermediate, but tends toward *Gila.*

TABLE 4. COMPARISONS OF ONE SPECIMEN OF GILA NIGRESCENS × RHINICHTHYS CATARACTAE WITH SPECIMENS OF THE PARENTAL SPECIES (MEANS ARE ABOVE, RANGES IN PARENTHESES BELOW)

	Gila nigrescens	KU 4253	*Rhinichthys cataractae*
Standard lengths	66.4 (63.1–72.4)	60.6	59.5 (55.6–65.0)
$\frac{\text{Head-length}}{\text{Standard length}}$	282 (277–290)	281	281 (273–293)
$\frac{\text{Orbital length}}{\text{Standard length}}$	063 (063–065)	054	044 (041–047)
$\frac{\text{Snout-length}}{\text{Standard length}}$	083 (081–085)	092	106 (099–113)
$\frac{\text{Dorsal fin-height}}{\text{Standard length}}$	225 (212–238)	234	221 (206–234)
$\frac{\text{Postorbital length}}{\text{Standard length}}$	140 (134–142)	135	131 (127–136)
$\frac{\text{Distance from tip of mandible to tip of maxillary}}{\text{Standard length}}$	081 (079–085)	076	066 (064–069)
$\frac{\text{Length of infralabial groove}}{\text{Standard length}}$	060 (058–064)	045	036 (034–038)
Upper jaw	protractile	non-protractile	non-protractile
Number scales in lateral line	60 (58–63)	63	65 (63–67)
Anal fin-rays	8 (7–8)	7	7 (7)
Pelvic fin-rays	9 (9)	8	8 (8–9)
Pectoral fin-rays	16 (16–18)	16–15	13 (13–14)
Pharyngeal teeth	2,5–4,2	2,5–4,2	2,4–4,2

TABLE 5. COMPARISONS OF ONE SPECIMEN OF NOTROPIS V. VENUSTUS × NOTROPIS WHIPPLEI WITH SPECIMENS OF THE PARENTAL SPECIES, AND WITH N. LUTRENSIS × N. V. VENUSTUS. MEASUREMENTS (LENGTHS AND DEPTHS) ARE EXPRESSED AS THOUSANDTHS OF STANDARD LENGTH (MEANS ABOVE, RANGES IN PARENTHESES BELOW)

	Notropis whipplei	KU 3516	*Notropis venustus*, KU 3510	*Notropis venustus* from Gibbs (1957a)	*Notropis lutrensis* × *N. venustus*
Standard length	50.6 (45.0–54.0)	47.8	47.3 (44.5–49.6)	....	44.7 (43.3–47.3)
Predorsal length	525 (513–535)	523	534 (519–547)	523	532 (528–538)
Dorsal origin to caudal base	497 (493–502)	508	497 (478–504)	496	508 (502–514)
Prepelvic length	505 (498–518)	492	505 (500–510)	....	499 (486–517)
Head-length	257 (250–262)	255	261 (256–267)	260	263 (261–267)
Caudal peduncle-length	217 (211–220)	221	224 (213–230)	....	224 (214–231)
Caudal peduncle-depth	110 (106–116)	119	127 (124–133)	125	126 (122–131)
Head-depth	170 (167–173)	182	186 (182–190)	....	190 (189–192)
Snout-length	079 (076–083)	079	080 (072–083)	....	081 (078–082)
Eye-diameter	069 (063–078)	069	070 (066–072)	073*	070 (068–074)
Postorbital length, head	112 (108–115)	115	116 (112–120)	....	117 (115–120)
Upper jaw, length	078 (076–081)	077	081 (076–082)	079	077 (076–081)
Body depth	239 (233–248)	253	278 (261–288)	274	282 (275–294)
Lateral-line scales	36–37	36	36–38	36.5 (34–39)	....
Scales above lateral-line	13	14	15	15 (13–16)	....

TABLE 5. COMPARISONS OF ONE SPECIMEN OF NOTROPIS V. VENUSTUS × NOTROPIS WHIPPLEI WITH SPECIMENS OF THE PARENTAL SPECIES, AND WITH N. LUTRENSIS × N. V. VENUSTUS. MEASUREMENTS (LENGTHS AND DEPTHS) ARE EXPRESSED AS THOUSANDTHS OF STANDARD LENGTH (MEANS ABOVE, RANGES IN PARENTHESES BELOW)—*Concluded*

	Notropis whipplei	KU 3516	*Notropis venustus,* KU 3510	*Notropis venustus* from Gibbs (1957a)	*Notropis lutrensis* × *N. venustus*
Anal fin-rays.......	9	9	8	8 (7–8)	....
Pectoral fin-rays....	14 (14–15)	14–14	15 (14–16)	14.2 (12–17)	....
Caudal spot.......	Absent	Present	Present	Present	Present
Vertebrae.........	37–38	38	37	....	....

* Orbital diameter.

The air bladder of KU 4253 is nearly as large as in *Gila,* and much larger than the degenerate air bladder of *R. cataractae.* Although the hybrid appears to be male, the gonads (especially the right one) are poorly developed. The hybrid is intermediate in curvature of the lateral line, which is nearly straight in *Rhinichthys* and strongly decurved in *Gila.*

Specimen No. 4253 is mostly pallid, resembling *Gila* much more than *Rhinichthys* in pigmentation. A mid-dorsal dark streak is conspicuous in the hybrid, especially anteriorly, but is less intense than in *Gila. Rhinichthys* lacks a well-developed dorsal stripe. The preorbital and suborbital areas are more heavily pigmented in the hybrid than in *Gila,* but not nearly so dark as in *Rhinichthys.* The hybrid has a faint dark basicaudal spot that is variably developed in *Rhinichthys* but absent in *Gila.*

Notropis venustus venustus × *Notropis whipplei:* KU 3516 (a male, 47.8 mm. in standard length), from Arkansas, Sevier Co., Winters Creek where it is crossed by U. S. Highway 71, 5 mi. N of Little River Bridge, March 8, 1956. Compared in Table 5 with four specimens of *N. whipplei,* KU 3517 (45.0-52.6 mm. in standard length, mean 50.6 mm.), same locality and date as KU 3516; four specimens of *N. v. venustus,* KU 3510 (44.5-49.6 mm. in standard length, mean 47.3 mm.), Louisiana, Winn Parish, Little Naches Bayou on U. S. Highway 71, 8.8 mi. NW Montgomery, March 4, 1956; three specimens of *Notropis lutrensis* (Baird and Girard) × *N. v. venustus,* KU 3510 (43.3-47.3 mm. in standard length, mean 44.7 mm.), same locality and date as *N. v. venustus* above; and with tabulated data on *N. v. venustus* from Gibbs (1957a:185-186). All specimens are from the lower Red River Drainage; other series of *N. whipplei, N. venustus,* and *N. lutrensis* × *N. venustus,* from the Red River Drainage and elsewhere, were examined but are not tabulated because of differences in size, and because of geographic variability that has been discussed by Gibbs (1957a).

The Subgenus *Cyprinella* of *Notropis,* to which *N. venustus* and *N. whipplei* belong, has been studied intensively by Gibbs (1957a and b). *Notropis venustus* differs conspicuously from *N. whipplei* in having a large dark basicaudal spot; also, *N. venustus* usually has 8 (rather than 9) anal rays, and 15 (rather than 13) scales above the lateral line immediately anterior to the dorsal fin. Specimens of *N. v. venustus* from the Red River Drainage, where the most robust representatives of the species are found, differ from *N. whipplei* in depth of head, body, and caudal peduncle (Table 5).

KU 3516 has a composite of the 9-rayed anal fin of *N. whipplei* and the caudal spot (albeit diffuse) of *N. venustus;* and, the hybrid is intermediate in body-proportions that distinguish the two species, especially depth of head, body, and caudal peduncle. In other features KU 3516 has values within the overlapping ranges of variation of *whipplei* and *venustus* except that the ratio of postdorsal length to standard length is extremely long in the hybrid, and the ratio of prepelvic length to standard length is extremely short (Table 5). Both extreme values for the hybrid seem to result from the cumulative influence of characters in which the parental species differ slightly in mean value (especially head-length, in which the hybrid is like *whipplei,* and caudal peduncle-length, in which the hybrid approaches *venustus,* despite the 9-rayed anal fin of the hybrid). The basicaudal spot of the hybrid is like that of *N. v. venustus* except for being less intense.

Notropis venustus hybridizes extensively with *N. lutrensis* (Hubbs, Kuehne, and Ball, 1953:226-230; Hubbs and Strawn, 1956), and that combination occurs in streams near the locality where KU 3516 was taken. KU 3516 resembles *N. lutrensis* × *N. v. venustus* in many ways, but is more slender than the latter hybrid. The depth of head, body, and caudal peduncle are greater in *N. lutrensis* than in *N. venustus* (much greater than in *N. whipplei*); therefore, specimens of *N. lutrensis* × *N. venustus* are usually deeper than *N. venustus*, whereas KU 3516 is less deep. KU 3516 has a rather sharp snout and thin, straight lips that are strongly suggestive of *N. whipplei*, rather than *N. lutrensis*, in which the snout is rounded and the lips are more obliquely decurved. There is less pigment underlying the anterior lateral-line scales in KU 3516 than in *N. lutrensis* × *N. venustus*, and melanophores on the scale-pockets of KU 3516 are arranged in narrower, more distinct submarginal bars than in *N. lutrensis* × *N. venustus*. Because of the difference in pigmentation, the lateral scales of *N. whipplei* (and of KU 3516) appear more narrowly diamond-shaped than the lateral scales of *N. lutrensis* or *N. lutrensis* × *N. venustus*. The lengths and heights of the scales are approximately the same in all three species.

Winters Creek, where KU 3516 was taken, flowed approximately five cubic feet per second at the time our collection was made; a landowner on the stream stated that it had been dry, except for pools, in the previous two summers. The water was somewhat gray, but nearly clear. The habitat consisted mainly of short riffles, with average depth of four inches, and pools to depths of two feet. Twelve species of fish, including *N. whipplei* but not *N. lutrensis* or *N. venustus*, were found; other minnows were *Semotilus atromaculatus*, *N. chalybaeus*, *N. cornutus*, *N. umbratilis*, and *Campostoma anomalum*.

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August 16, 1960

A Distributional Study of the Amphibians of the Isthmus of Tehuantepec, México

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WILLIAM E. DUELLMAN

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10. A new bat (Genus Pipistrellus) from northeastern Mexico. By Rollin H. Baker. Pp. 583-586. November 15, 1954.

11. A new subspecies of pocket mouse from Kansas. By E. Raymond Hall. Pp. 587-590. November 15, 1954.

12. Geographic variation in the pocket gopher, Cratogeomys castanops, in Coahuila, Mexico. By Robert J. Russell and Rollin H. Baker. Pp. 591-608. March 15, 1955.

13. A new cottontail (Sylvilagus floridanus) from northeastern Mexico. By Rollin H. Baker. Pp. 609-612. April 8, 1955.

14. Taxonomy and distribution of some American shrews. By James S. Findley. Pp. 613-618. June 10, 1955.

15. The pigmy woodrat, Neotoma goldmani, its distribution and systematic position. By Dennis G. Rainey and Rollin H. Baker. Pp. 619-624, 2 figures in text. June 10, 1955.

Index. Pp. 625-651.

(Continued on inside of back cover)

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CONTENTS

INTRODUCTION

Few regions in Middle America are so important zoogeographically as is the Isthmus of Tehuantepec, that neck of land connecting North America with Central America, separating the Pacific Ocean from the Gulf of Mexico by a distance of only about 220 kilometers (airline), and forming a low break between the highlands of México and those of Central America. Before World War II the isthmus could be reached readily only by railroad or by ocean vessel to Salina Cruz or Coatzacoalcos. With the advent of roads, principally the Trans-isthmian Highway, vast areas of the interior of the isthmus became accessible to biologists. Nevertheless, long before roads were built in the isthmian region collectors and biologists visited it, especially the town of Tehuantepec, from which collections date back to the 1870's. Therefore, it is rather surprising that no attempt has been made to present a faunal list of the amphibians or reptiles of the isthmus. Ruthven (1912) summarized his collections from the vicinity of Cuatotolapam, Veracruz, and Hartweg and Oliver (1940) presented an annotated list of the species collected by them in the vicinity of Tehuantepec. In recent years there have been only a few papers reporting species from the isthmus (Fugler and Webb, 1957; Langebartel and Smith, 1959). The zoogeographic significance of the Isthmus of Tehuantepec is exemplified by the works of Burt (1931), Duellman (1958), Gloyd (1940), Oliver (1948), and Stuart (1941), who in their discussions of evolution and dispersal of various genera of reptiles, pointed out that the Isthmus of Tehuantepec was a region of zoogeographic importance.

Originally I intended to study the entire herpetofauna of the isthmus. But I have not had opportunity to study all of the reptiles, and I have not had the inclination to solve certain taxonomic problems concerning them. The amphibians that I collected, together with all other known specimens in museums, have been studied. Therefore, the present report is concerned only with the amphibians. Only the amphibians of the lowlands of the isthmus have been sampled adequately. Although I have commented on the highland species in the discussion of distribution, they are not included in the systematic section, which deals solely with the 36 species definitely known to occur in the lowlands of the isthmus.

Among the species of amphibians that I would expect to occur in the isthmus, the only one not yet found there is *Hyla phaeota*. Sufficient specimens of most of the species are available to show their variation in the isthmus. Consequently, the systematics of these amphibians is on a fairly substantial basis. Probably certain species in the isthmian region will be found to be conspecific with others to the south, for example *Hyla ebraccata* with *Hyla leucophyllata* and *Hyla robertmertensi* with *Hyla underwoodi*. Nevertheless, such taxonomic changes will not affect the distributional picture presented here. Our greatest lack of knowledge concerning the amphibians is about their life histories, as may be illustrated by the following questions, all of which now are without definite answers. Where do many of the small frogs conceal themselves during the dry season? What amount of, if any, interspecific competition exists among several species of tree frogs, all of which breed in the same ponds? What factors in the environment permit certain amphibians, but not others, to live in the humid rainforests, as well as in the arid tropical scrub forest? The answers to these questions and many others must await additional field studies.

The purpose of this paper is to make known the species of amphibians living in the Isthmus of Tehuantepec, to describe the environments in which they live, and to discuss their distribution in the isthmus. With respect to the distribution of animals in the Isthmus of Tehuantepec I will attempt to explain the present patterns of distribution with special reference to climatic fluctuation in the Pleistocene.

Acknowledgments

My extensive field work in the Isthmus of Tehuantepec was made possible by grants from the Penrose Fund of the American Philosophical Society (1956) and the Bache Fund of the National Academy of Sciences (1958). Furthermore, my field work received the hearty support of the Museum of Zoology at the University of Michigan; for their cooperation I am indebted to Norman Hartweg, T. H. Hubbell, and Henry van der Schalie. In the course of my studies I received helpful suggestions from Norman Hartweg, L. C. Stuart, and Charles F. Walker, to whom I am grateful. For permission to examine specimens in their care I thank Doris M. Cochran, Hobart M. Smith, and Richard G. Zweifel. I am deeply indebted to Thomas MacDougall for many suggestions and for aid in preparing the gazetteer. I am most grateful for the efforts of my field companions, Richard E. Etheridge, Jerome B. Tulecke, John Wellman, and especially my wife, Ann S. Duellman, who spent many long days and nights gathering much of the data on which this report is based. Our work in the isthmus was furthered by the generous help and hospitality of many residents, especially the late Wilbur Barker of Tehuantepec, Fortunado Delgado of Rancho Las Hojitas near Acayucan, César Fárjas of Donají, and Juan Mayol of San Andrés Tuxtla. Profesor Jordi Juliá Z. of the Laboratorio de Entomología, Comisión del Papaloapan, Ciudad Alemán, Veracruz, helped make possible my field work in 1959; for this he has my sincere thanks. In conclusion I express my gratitude to Ing. Juan Lozano Franco, Secretaria de Agricultura y Ganadería, for providing me with the necessary permits.

Field Studies in the Isthmus of Tehuantepec

I first visited the Isthmus of Tehuantepec and collected on the Pacific lowlands of the isthmus in July, 1955. At that time heavy rains and impassable roads restricted travelling. In February and March of 1956 my wife and I concentrated our efforts in the central region between the Río Jaltepec and Matías Romero, but also made several trips across the isthmus to gather ecological data in the dry season. In July of the same year, accompanied by Richard E. Etheridge, we again crossed the isthmus several times in order to gather ecological data in the wet season, and studied especially hylid frogs, most of which had not been seen in the dry season. Accompanied by Jerome B. Tulecke and John Wellman, I collected again in the isthmus in July, 1958, between Salina Cruz and Tehuantepec, and between Coatzacoalcos and Cosoleacaque. In March and April, 1959, I collected at Ciudad Alemán. Nearly 1200 specimens of 30 species of amphibians were thus collected in the Isthmus of Tehuantepec; all specimens are now in the Museum of Zoology at the University of Michigan. Of other species known from the isthmus, I have had field experience with all but one *(Bolitoglossa veracrucis)* in other parts of México.

Sources of Material

There are in museum collections nearly 3000 specimens of amphibians with reliable data from the Isthmus of Tehuantepec. Among the first herpetological specimens collected in the isthmian region are those assembled by Francis Sumichrast in the 1870's from the vicinity of Santa Efigenia and Tapanatepec, Oaxaca. These specimens were sent to the United States National Museum and the Museum National d'Histoire Naturelle in Paris; many served as the types of new species: *Bufo canaliferus* Cope, *Eleutherodactylus rugulosus* Cope, *Syrrhophus leprus* Cope, and *Hylella sumichrasti* Brocchi. In 1911 Alexander G. Ruthven collected in the savanna country near Cuatotolapam, Veracruz; the report on his collections (1912) is the first dealing with the herpetofauna of a part of the isthmus. His specimens are in the collection of the University of Michigan Museum of Zoology. Norman Hartweg and James A. Oliver collected for the University of Michigan Museum of Zoology in the vicinity of Tehuantepec, Oaxaca, during the summer of 1936. The results of their work were published as an annotated list of species occurring on the Pacific slopes of the isthmus (1940). Hobart M. Smith collected in the vicinity of Tehuantepec in January, 1940; his specimens are in the United States National Museum. Specimens collected by Smith served as the types of *Eleutherodactylus avocalis* Taylor and Smith and *Diaglena reticulata* Taylor. Walter W. Dalquest collected vertebrates for the University of Kansas in southern Veracruz in the winters of 1947 and 1948; he spent about six months on the Gulf lowlands of the isthmus, principally in the vicinity of Jesús Carranza. For the past two decades Thomas MacDougall, a resident of New York City, has spent his winters collecting biological specimens in southern México. He makes his headquarters at Tehuantepec, but his compulsion to see the "back country" has taken him to many remote parts of southern Oaxaca. His earlier collections are in the American Museum of Natural History; the later ones are in the University of Illinois Museum of Natural History.

Minor collections include those made by Matthew W. Stirling at San Lorenzo, Veracruz, February-April, 1946 (United States National Museum), by Fred G. Thompson on a trip across the isthmus in December, 1955 (University of Michigan Museum of Zoology), by the University of Kansas Museum of Natural History field party under the direction of Rollin H. Baker at Tolosita, Oaxaca, and by David A. Langebartel and associates from southern Oaxaca in June, 1958 (University of Illinois Museum of Natural History).

In the collections of the United States National Museum are several species of amphibians sent to the museum from Tehuantepec by Francis Sumichrast. These include *Bolitoglossa platydactyla* (USNM 30305, 30344-6, 30528), *Bolitoglossa rufescens* (10042), *Chiropterotriton chiropterus* (30347), *Lineatriton lineola* (30353), *Parvimolge townsendi* (30352), *Pseudoeurycea cephalica* (30350), *Thorius pennatulus* (30348-9), *Hyla miotympanum* (30302-3), and *Hyla picta* (30304). Because of the poor condition of the specimens, determinations of those listed as *Bolitoglossa rufescens* and *Pseudoeurycea cephalica* are uncertain. With the exception of the *Bolitoglossa rufescens,* which is stated to have come from Santa Efigenia, all of these specimens are catalogued as having come from Tehuantepec. None of these species has since been recorded from the Pacific slopes of the isthmus; however, they all occur in the vicinity of Orizaba, Veracruz. Probably Sumichrast carried the specimens with him from Orizaba, his home before moving to Santa Efigenia, and shipped them from Tehuantepec to the United States National Museum. These species definitely should not be considered as inhabitants of the Pacific slopes of the Isthmus of Tehuantepec.

DESCRIPTION OF THE ISTHMUS OF TEHUANTEPEC

The Isthmus of Tehuantepec is a strip of land forming a low pass, which separates the mountain masses of México proper from those of Central America, and at the same time provides a continuum of lowlands from the Gulf of Mexico to the Pacific Ocean. This topography combines with the climatic conditions to create extremely diverse environments, the distribution of which can be adequately understood only after an acquaintance with the topography and climate of the region.

Physiography

In east-central Oaxaca the mountain masses comprising the Sierra Madre Oriental and the Sierra del Sur terminate in a series of ranges—Sierra de Juárez, Sierra de los Míjes, and Sierra de Choapam. From lofty peaks, such as Cerro de Zempoaltepetl (3400 meters), the highlands diminish eastward to succeedingly lower ridges, until in the middle of the Isthmus of Tehuantepec the continental divide is about 250 meters above sea level. Eastward from this low divide the land rises to form the Sierra Madre de Chiapas, which is continuous with the highland masses of Guatemala.

For the purposes of this description, the lowlands of the isthmus may be divided into three parts—the Gulf Coastal Plain, the central ridges, and the Pacific Coastal Plain, which in the isthmus is called the Plains of Tehuantepec (Figs. 1 and 2).

The Gulf Coastal Plain is broad and fairly level near the coast, but rolling in the interior. The plain, throughout most of its length in the isthmus, is at least 75 kilometers wide. The majority of the region in the isthmus is drained by the Río Coatzacoalcos, which flows in a northerly course to the Gulf of Mexico. The western part is drained by the Río San Juan, the principal tributary of the Río Papaloapan. Behind the coastal dunes are frequent, and some-

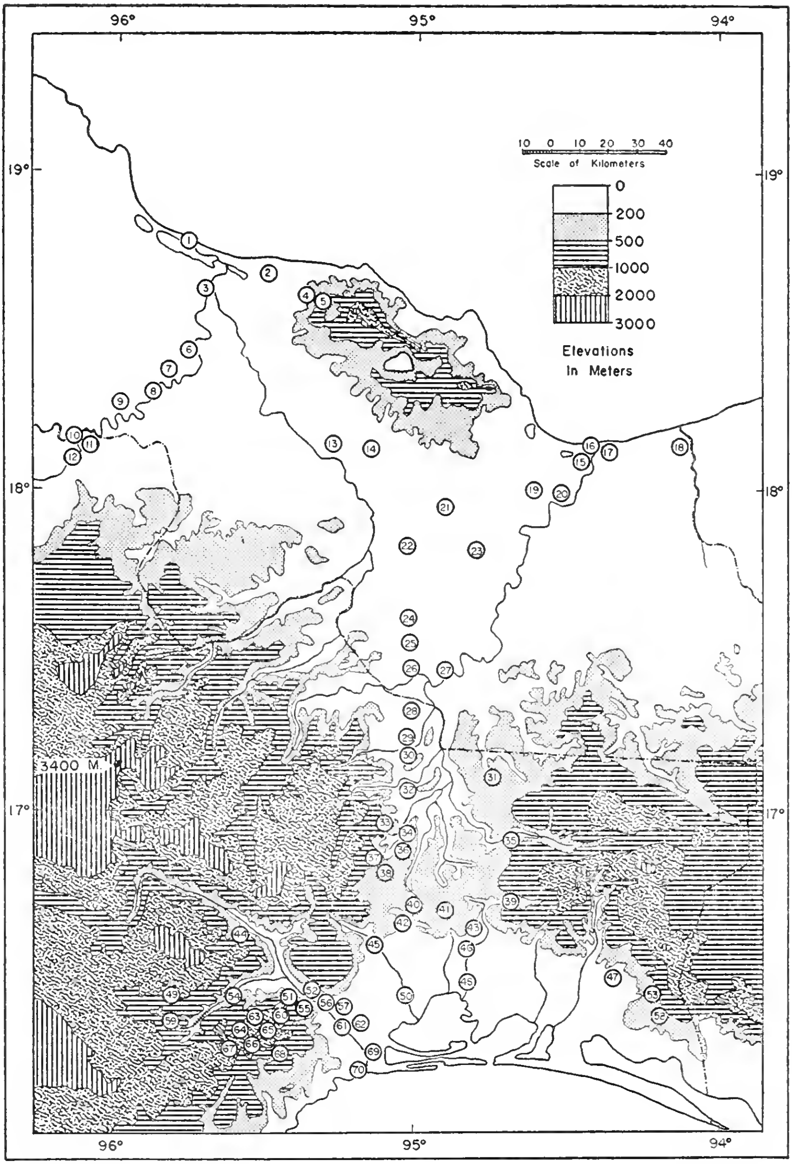

FIG. 1. Map of the Isthmus of Tehuantepec based on the American Geographical Society's "Map of Hispanic America on the Scale of 1:1,000,000."

The localities shown are numbered in the gazetteer; the numerical sequence of localities is an arrangement whereby north takes precedence over south and west over east. 1. Alvarado. 2. Lerdo de Tejada. 3. Tlacotalpan. 4. Tula. 5. Tecolapan. 6. Amatitlán. 7. Cosamaloapan. 8. Chacaltianguis. 9. Novillero. 10. Ciudad Alemán. 11. Papaloapan. 12. Tuxtepec. 13. Cuatotolapam. 14. Hueyapan. 15. Berta. 16. Coatzacoalcos. 17. Ayentes. 18. Río de las Playas. 19. Cosaleacaque. 20. Minatitlán. 21. Acayucan. 22. Aquilera. 23. San Lorenzo. 24. Naranja. 25. Suchil. 26. Jesús Carranza. 27. La Oaxaqueña. 28. Ubero. 29. Donají. 30. Tolosita. 31. El Modelo. 32. Sarabia. 33. Guichicovi. 34. La Princesa. 35. Santa María Chimalapa. 36. Matías Romero. 37. Santo Domingo Petapa. 38. El Barrio. 39. Palmar. 40. Chivela. 41. Santiago Chivela. 42. Nizanda. 43. Agua Caliente. 44. Portillo Los Nanches. 45. Ixtepec. 46. La Ventosa. 47. Zanatepec. 48. Unión Hidalgo. 49. Tres Cruces. 50. Juchitán. 51. Escurano. 52. Salazar. 53. Santa Efigenia. 54. Tequisistlán. 55. Cerro de Quiengola. 56. San Pablo. 57. Mixtequilla. 58. Tapanatepec. 59. Zarzamora. 60. Limón. 61. Tehuantepec. 62. Bisilana. 63. Santa Lucía. 64. Cerro de Arenal. 65. Cerro de San Pedro. 66. La Concepción. 67. Tenango. 68. San Antonio. 69. Huilotepec. 70. Salina Cruz.

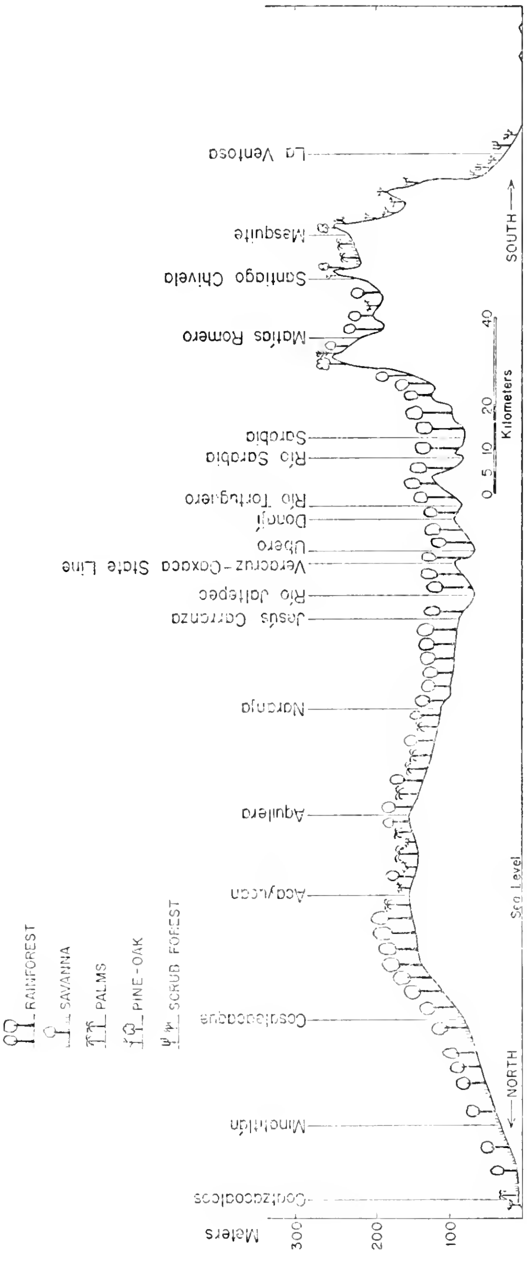

FIG. 2. Topographic profile of the Isthmus of Tehuantepec showing major localities along the Trans-isthmian Highway and major types of vegetation. Vertical exaggeration approximately 165 times.

times large, lagoons. Immediately inland from Coatzacoalcos and along the lower stretches of the Río Papaloapan are extensive marshes. Essentially the entire coastal plain, with the exception of the coastal dunes, consists of rich alluvial deposits.

The central ridges extend from the Río Jaltepec southward to within 40 kilometers of the Pacific coast. It is in this area that the continuity of the high ridges and volcanic peaks, which extend nearly the entire length of the Americas, is interrupted at a point almost directly in line with the shortest distance between the two oceans. The northern part of this central region consists of hills dissected by tributaries of the Río Coatzacoalcos; the principal ones from north to south are—Río Jaltepec, Río Tortuguero, Río Sarabia, and Río Malatengo. The plains of Chivela are south of these rivers and lie at an elevation of about 200 meters; at the southern edge of these plains a range of hills rises to 250 to 400 meters above sea level. These hills drop abruptly to the Plains of Tehuantepec. In the northern and central parts of this central region the rocks are granitic; the hills to the south of the Plains of Chivela are limestone.

The Pacific Coastal Plain or Plains of Tehuantepec have a maximum width of about 30 kilometers. From the base of the hills at an elevation of about 75 meters the plains slope gradually to the sea. To the west of the Río Tehuantepec and to the east of the Plains of Tehuantepec at the base of the Sierra Madre de Chiapas, the coastal plain becomes much narrower; in these places the continuity of the plain is frequently interrupted by low north-south ridges extending outward from the mountains or by isolated hills. The soil is poor, varying from volcanic rock to gravel and sand.

Climate

The prevailing winds are from the north across the Gulf of Mexico. These moisture-laden winds precipitate most of their moisture north of the central ridges. This results in high rainfall on the northern slopes and Gulf Coastal Plain and relatively little rainfall on the southern slopes and the Pacific Coastal Plain. Precipitation is cyclic; there is a marked wet and a dry season throughout the region, but this is most noticeable on the Pacific lowlands (Fig. 3). At Salina Cruz on the Pacific Ocean the average annual rainfall is 1040 mm. (Contreras, 1942); of this amount, only 15 mm. falls from November through April. On the Gulf Coastal Plain (Minatitlán station) the average annual

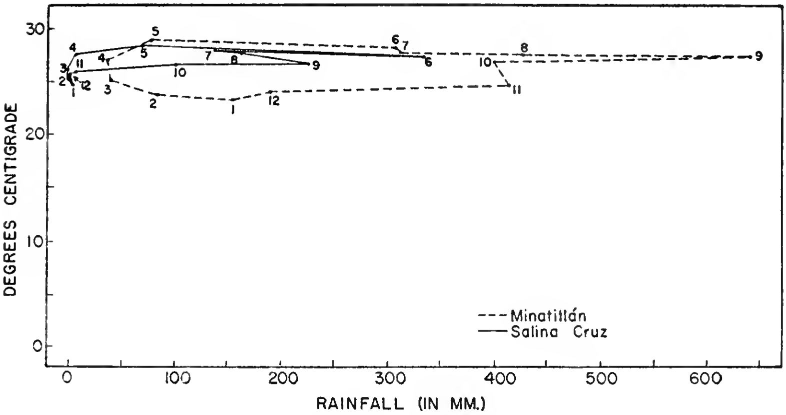

FIG. 3. Climatographs for Minatitlán, Veracruz, and Salina Cruz, Oaxaca, based on data given by Contreras (1942). Plotted points are for mean monthly temperatures and rainfall; months are indicated by numbers.

rainfall is 3085 mm. In this region the driest months are February through May, during which time 236 mm. of rain falls. At Salina Cruz the wettest month is June; at Minatitlán it is September. There is little variation in temperature throughout the isthmus; the average annual temperature at Salina Cruz is 26.6° C.; that at Minatitlán is 26.2° C. During the winter when masses of air from the arctic move southward into the Great Plains of the United States, cool winds blow across the isthmus. These are usually accompanied by overcast sky and sometimes a slight amount of precipitation. These "nortes" may cause a drop in temperature of about six to eight degrees in a few hours.

Vegetation

The topography and climate combine to produce drastically different types of climax vegetation on the northern and southern lowlands of the isthmus. The picture is somewhat complicated by the savannas on the Gulf Coastal Plain, which, as will be shown later, are dependent upon edaphic features more than climatic conditions. The following brief account of the vegetation in the Isthmus of Tehuantepec is based on data provided by Williams (1939) and Goldman (1951), supplemented by personal observations. The purpose of this description is not to analyze the flora of the isthmus, but to give the reader a picture of this aspect of the biota of the major environments with which I shall be concerned in the ensuing discourse on the amphibians of the region.

The three divisions of the isthmus recognized in the account of the physiography serve equally well in describing the vegetation. Those divisions are as follows:

Gulf Lowlands

On the lowlands north of the continental divide and extending to the Gulf of Mexico are three major types of vegetation—tropical rainforest, arid tropical scrub forest, and savanna. Aside from these, there are marshes and lagoons near the coast.

On the coastal dunes there are thickets of sea grape, patches of *Cenchrus*, and clumps or scattered *Opuntia.* The lagoons are bordered by mangrove thickets made up primarily of *Lonchocarpus hondurensis.* In the marshes along the lower Río Coatzacoalcos and Río Papaloapan the tall tough grass, *Gynerium sagittatum,* is common.

According to Beard (1953: 291) the development of savanna vegetation is dependent upon soil, topography, and drainage. Level regions having permeable soil horizons lying on top of an impermeable horizon provide poor drainage. In most savanna regions in the Americas the grasslands become waterlogged or even partly flooded during the rainy season and desiccated in the dry season. Many ecologists and phytogeographers have postulated that savannas are either man made or are examples of a fire climax. Beard (*op. cit.:* 203) provided multitudinous evidence that the association of savanna vegetation and certain types of edaphic and topographic conditions was so strongly marked that grassland is the natural vegetation in these areas.

Savannas are scattered through southern Veracruz eastward to British Honduras. These usually are grasslands having scattered trees or clumps of trees around depressions, which may contain water throughout the year (Pl. 1, fig. 1). According to Williams (*op. cit.*), the most common trees in the savannas in southern Veracruz are *Ceiba pentandra, Chlorophora tinctoria,* and *Brysonima crassifolia.*

Lying in a rain shadow cast by the Tuxtlas and on sandy and well-drained soils is a dense xerophytic forest. The crown of this deciduous forest usually is little more than ten to twelve meters above the ground (Pl. 1, fig. 2). Conspicuous trees in this scrub forest are *Acacia cornigera, Bauhinia latifolia, Calliandra bijuga, Cassia laevigata, Guazuma ulmifolia,* and various species of *Bursera.*

The most extensive type of vegetation on the Gulf Coastal Plain is a tall evergreen forest resembling tropical rainforest. Although this forest is made up of many species of trees that are characteristic of true rainforest, the forest on the Gulf Coastal Plain cannot be classified as true rainforest, neither by the climatic conditions, nor the structure of the forest. The seasonal variation in rainfall probably is the chief factor in hindering the development of a rainforest climax vegetation. Usually a minimum of 65 mm. of rainfall each month is considered essential for the development of true rainforest. At Minatitlán the average rainfall for March (39 mm.) and April (36 mm.) is far below this minimum. Structurally, this forest has a crown about 30-35 meters above the ground but individual trees rising five meters or more above the crown (Pl. 2, figs. 1-2). There is no clear stratification within the forest; in many parts of it there are dense growths of bushes, small trees, and palms. The forest on the Gulf Coastal Plain, therefore, most properly might be referred to as a quasi-rainforest, a term that has been applied to other such forests in tropical America.

Among the abundant and dominant trees in this forest are *Swietenia macrophylla, Calophyllum brasiliense, Achras zapota, Ceiba pentandra, Castilla elastica, Cedrela mexicana, Tabebuia Donnell-Smithi, Calocarpum mammosum, Bombax ellipticum,* and a variety of *Ficus.* Epiphytes and llianas are abundant.

Central Ridges

The vegetation of the central ridges of the isthmus is, for the most part, transitional between the tall rainforest of the Gulf Coastal Plain and the low xerophytic scrub forest of the semi-arid Pacific Coastal Plain. On the northern slopes of the ridges the rainforest is more poorly developed than on the plains to the north. Many of the same species of trees are present, including *Ceiba pentandra, Cedrela mexicana, Swietenia macrophylla,* and *Ficus* sp.; nevertheless, these seldom are as large as members of the same species in the forest on the plains. Other species present on the forested slopes include *Tabebuia Donnell-Smithi, Zanthoxylum melanostictum, Pithecolobium arboreum,* and a species of *Pterocarpus.* The structure of this forest differs from that on the Gulf Coastal Plain in that there is no continuous upper canopy and there is a dense undergrowth (Pl. 3, fig. 1). This type of forest extends from Mogoñe southward to about Matías Romero.

In the vicinity of Matías Romero open pine-oak forest (*Pinus caribaea* and *Quercus* sp.) is found on some ridges as low as 250 meters above sea level.

On the Plains of Chivela in the southern part of the central region the vegetation takes on a semi-arid appearance, especially in a savanna on the plains. Clumps of small trees and bushes, consisting of *Croton nivea, Cordia cana, Jacquinia aurantiaca, Calycophyllum candidissimum,* and *Cassia emarginata,* are scattered on a grassy plain, from which rise widely-spaced palms of an unknown species (Pl. 3, fig. 2).

Pacific Coastal Plain

The vegetation of the Pacific lowlands definitely is semi-arid in character. Most of the trees are deciduous, thorny, and short. During the dry season the landscape presents a barren appearance, but shortly after the first summer rains dense green foliage appears (Pl. 4, figs. 1 and 2). Between Juchitán and La Ventosa few trees are more than two meters high (Pl. 5, fig. 1). In many areas the trees and bushes form an almost impenetrable tangle, whereas on especially rocky soils or on slopes those plants are more widely spaced. Abundant and widespread species of trees on the Plains of Tehuantepec include *Acacia cymbispina, Prosopis chilensis, Caesalpinia coriaria, Caesalpinia eriostachys, Celtis iguanaea, Cordia brevispicata, Jatropha aconitifolia,* and *Crescentia alata.*

Montane Vegetation

In order to illustrate the interruption of subtropical and temperate types of vegetation by the lowlands of the Isthmus of Tehuantepec, it is necessary to digress for a moment from the isthmus and consider the types of vegetation present on the adjacent highlands. On the higher peaks, such as Cerro de Zempoaltepetl, above about 2500 meters is fir forest (*Abies religiosa*); lower on the slopes are extensive pine forests, which on some slopes are mixed with oak or replaced entirely by oaks. Subtropical cloud forest, characterized by relatively cool temperatures and high humidity, is found at elevations usually between 1000 and 1800 meters on the windward slopes of the Sierra Madre Oriental in Veracruz and northern Oaxaca and on the northern and southern slopes of the Chiapan-Guatemalan Highlands. None of these forest types is continuous across the Isthmus of Tehuantepec.

The Sierra de los Tuxtlas

Although actually located in the region of the Isthmus of Tehuantepec, the Sierra de los Tuxtlas, because of its isolated position, need not be considered in great detail in analyzing the distribution of animals inhabiting the lowlands of the isthmus. Nevertheless because some species living in the highlands adjacent to the isthmus also live in the Tuxtlas, this range is briefly described here. The Sierra de los Tuxtlas is a range of volcanos lying near the Gulf Coast in southern Veracruz between the mouths of the Río Papaloapan and the Río Coatzacoalcos. Volcán San Martín, the highest peak, rises above 1800 meters. This range of volcanos is surrounded by lowlands, which immediately to the south and west are covered with savanna and in places by scrub forest. The luxuriant nature of the vegetation on these volcanos indicates that this range receives much more rainfall than the surrounding lowlands. Especially on the northern slopes, tropical rainforest is well developed; this is replaced at about 1200 meters by cloud forest. The southern and western slopes are drier, for the lower slopes are covered with a scrubby, but evergreen, forest.

Detailed comments on the herpetofauna of the Tuxtlas have been omitted purposefully, for the reptiles and amphibians of the region currently are being studied by Douglas Robinson.

GAZETTEER

The following localities are those referred to in the text. The name of the locality (listed alphabetically by states) is followed by latitude, longitude, elevation, general description (town, ranch, etc.), and general type of habitat. Unless otherwise noted, distances are straight-line (airline) distances in kilometers. The localities have been plotted from the American Geographical Society's "Map of Hispanic America on the Scale of 1:1,000,000" (Millionth Map). Numbers in brackets identify the position of a locality on the accompanying map (Fig. 1).

Oaxaca

Agua Caliente.—Lat. 16° 38′; long. 94° 48′; elev. 140 m. A hot spring, 6.9 km. north of La Ventosa on the Trans-Isthmian Highway; arid scrub forest [43].

Arenal, Cerro de.—Lat. 16° 18′; long. 95° 32′; elev. 925 m. (crest). A ridge northeast of Tenango; scrub forest on slopes and pine-oak forest on top [64].

Barrio, El.—Lat. 16° 38′; long. 95° 07′; elev. 314 m. A village about 10 kilometers southwest of Matías Romero; transition between scrub forest and broadleaf hardwood forest [38].

Bisilana.—Lat. 16° 20′; long. 95° 13′; elev. 35 m. A place name for a former ranch at the edge of Tehuantepec; open arid scrub forest [62].

Chivela.—Lat. 16° 20′; long. 95° 01′; elev. 195 m. A village on the Trans-isthmian Railroad, 26 kilometers by rail south of Matías Romero and on the western edge of the semi-arid Plains of Chivela [40].

Concepción.—Lat. 16° 17′; long. 95° 29′; elev. 1200 m. A ranch on the slopes of Cerro Arenal, east-northeast of Tenango; dry pine-oak forest [66].

Coyol.—Exact position unknown; according to Smith and Taylor (1950: 10), Coyol is "between San Antonio and Las Cruces."

Donají.—Lat. 17° 13′; long. 95° 02′; elev. 90 m. A village at Km. 155 on the Trans-isthmian Highway; rainforest [29].

Escurano.—Lat. 16° 25′; long. 95° 27′; elev. 500 m. A ranch about 25 kilometers west-northwest of Tehuantepec; arid scrub forest [51].

Guichicovi, San Juan.—Lat. 16° 58′; long. 95° 06′; elev. 250 m. A village on the north slopes of the isthmus, 12 kilometers north-northwest of Matías Romero; cleared hardwood forest and coffee plantations [33].

Huilotepec.—Lat. 16° 14′; long. 95° 09′; elev. 30 m. A small village on the Río Tehuantepec, 13 kilometers south-southeast of Tehuantepec; open arid scrub forest [69].

Ixtepec.—Lat. 16° 34′; long. 95° 06′; elev. 60 m. A town and railroad junction on the northwestern edge of the Plains of Tehuantepec; arid scrub forest [45].

Juchitán.—Lat. 16° 26′; long. 95° 02′; elev. 15 m. A town on the Plains of Tehuantepec, 22 kilometers by road east-northeast of Tehuantepec; arid scrub forest [50].

Limón.—Lat. 16° 20′; long. 95′ 29°; elev. 600 m. A former agrarian colony and now a small ranch about 27 kilometers west of Tehuantepec; arid scrub forest [60].

Matías Romero.—Lat. 16° 53′; long. 95° 02′; elev. 200 m. A town on the Trans-isthmian Highway and railroad in the hills near the crest of the isthmus; broadleaf hardwood forest and open pine-oak forest [36].

Mixtequilla.—Lat. 16° 24′; long. 95° 18′; elev. 40 m. A village on the Río Tehuantepec, northwest of Tehuantepec; dense scrub forest [57].

Modelo, El.—Lat. 17° 07′; long. 94° 43′; elev. 200 m. An old rubber plantation on the Río Chalchijapa, a tributary to the Río Coatzacoalcos; rainforest [31].

Nanches, Portillo Los.—Lat. 16° 35′; long. 95° 37′; elev. 500 m. A place name, about 4 kilometers southeast of Totolapilla; scrub forest [44].

Nizanda.—Lat. 16° 42′; long. 95° 02′; elev. 150 m. A village on the Trans-isthmian Railroad between Chivela and Ixtepec; dense scrub forest [42].

Nueva Raza.—Exact location unknown; according to Thomas MacDougall, this locality is in the lowlands of northern Oaxaca; rainforest.

Palmar.—Lat. 16° 43′; long. 94° 40′; elev. 300 m. A small ranch on the west base of Cerro Atravesado; scrub forest [39].

Papaloapan.—Lat. 18° 11′; long. 96° 06′; elev. 25 m. A small village on the Río Papaloapan in northern Oaxaca; low evergreen forest and savanna [11].

Princesa, La.—Lat. 16° 56′; long. 95° 02′; elev. 150 m. A ranch on the northern slopes of the isthmus, 6 kilometers by road north of Matías Romero; poorly developed rainforest [34].

Quiengola, Cerro de.—Lat. 16° 24′; long. 95° 22′; elev. 900 m. (crest). A hill 15 kilometers west-northwest of Tehuantepec; dense scrub forest on slopes and scattered pines on top [55].

Salazar.—Lat. 16° 25′; long. 95° 20′; elev. 45 m. A ranch on the Río Tehuantepec, northwest of Tehuantepec; dense scrub forest [52].

Salina Cruz.—Lat. 16° 10′; long. 95° 12′; sea level. A port on the Golfo de Tehuantepec; open arid scrub forest [70]. Collections were made in the vicinity of the town and in the open scrub forest 2.4 kilometers north at an elevation of 20 meters.

San Antonio.—Lat. 16° 15′; long. 95° 22′; elev. 40 m. A ranch about 25 kilometers west-southwest of Tehuantepec; arid scrub forest [68].

San Pablo.—Lat. 16° 24′; long. 95° 18′; elev. 40 m. A ranch on the Río Tehuantepec, northwest of Tehuantepec; dense scrub forest [56]. Cerro San Pablo probably is the hill north of this ranch; this is shown on some maps as Cerro de los Amates.

San Pedro, Cerro de.—Lat. 16° 18′; long. 95° 28′; elev. about 1100 m. (crest). A ridge about 24 kilometers west of Tehuantepec and east of Cerro Arenal; scrub forest on slopes and pine-oak forest on top [65].

Santa Efigenia.—Lat. 16° 25′; long. 94° 13′; elev. 500 m. A ranch on the southern slopes of the Sierra Madre de Chiapas, 8 kilometers north-northwest of Tapanatepec; scrub forest. Former home of Francis Sumichrast [53].

Santa Lucía.—Lat. 16° 18′; long. 95° 28′; elev. 800 m. A place name for a former ranch on the east slopes of Cerro Arenal; scrub forest [63].

Santa María Chimalapa.—Lat. 16° 55′; long. 94° 42′; elev. 296 m. A village on the Río de los Milagros, a tributary to the Río Coatzacoalcos; rainforest [35].

Santiago Chivela.—Lat. 16° 42′; long. 94° 53′; elev. 200 m. A village on the Trans-isthmian Highway, 13.4 kilometers by road south of Matías Romera; dry, grassy plains and scattered clumps of scrubby trees and palms [41]. Collections were made in the vicinity of the village and at a rocky stream, 11 kilometers south on the Trans-isthmian Highway at an elevation of 230 m.

Santo Domingo (Petapa).—Lat. 16° 50′; long. 95° 08′; elev. 225 m. A village about 13 kilometers west-southwest of Matías Romero; semi-arid scrub forest [37].

Sarabia.—Lat. 17° 04′; long. 95° 02′; elev. 100 m. A village 25 kilometers north of Matías Romero on the Trans-isthmian Highway; rainforest [32]. Collections were made in the vicinity of the village and in the rainforest along the Río Sarabia, 5 kilometers north of the village at an elevation of 80 meters.

Tapanatepec.—Lat. 16° 32′; long. 94° 12′; elev. 90 m. A town on the Pan-American Highway on the lower slopes of the Sierra Madre de Chiapas; dense scrub forest [58].

Tehuantepec.—Lat 16° 20′; long. 95° 14′; elev. 35 m. A large town on the Plains of Tehuantepec; scrub forest [61]. Collections were made in the vicinity of the town and in the dense scrub forest 8.6 kilometers west at an elevation of 85 meters and 14 kilometers west at an elevation of 120 meters.

Tenango.—Lat. 16° 16′; long. 95° 30′; elev. 1100 m. A town in the mountains about 40 kilometers west-southwest of Tehuantepec; scrub forest [67].

Tequisistlán.—Lat. 16° 24′; long. 95° 37′; elev. 190 m. A village in the valley of the Río Tequisistlán, a tributary to the Río Tehuantepec; dense scrub forest [54]. Most collections were made about one kilometer north of the village where the Pan-American Highway crosses the Río Tequisistlán.

Tolosita.—Lat. 17° 12′; long. 95° 03′; elev. 80 m. A village on the Río Tortuguero near the Trans-isthmian Highway; rainforest [30].

Tres Cruces.—Lat. 16° 26′; long. 95° 51′; elev. 750 m. A ranch near the Pan-American Highway, 70 kilometers by road west-northwest of Tehuantepec; dense scrub forest [49].

Tuxtepec.—Lat. 18° 06′; long. 96° 05′; elev. 80 m. A town on the Río Papaloapan in northern Oaxaca; low evergreen forest [12].

Ubero.—Lat. 17° 18′; long. 95° 00′; elev. 80 m. A lumber camp and railroad station, 8.5 kilometers south of the Río Jaltepec on the Trans-isthmian Highway; rainforest [28].

Unión Hidalgo.—Lat. 16° 27′; long. 94° 48′; elev. 7 m. A village on the railroad, 20 kilometers east-northeast of Juchitán; open scrub forest [48].

Ventosa, La.—Lat. 16° 30′; long. 94° 51′; elev. 25 m. A village at the junction of the Pan-American and Trans-isthmian highways; open scrub forest [46].

Zanatepec.—Lat. 16° 28′; long. 94° 22′; elev. 80 m. A village on the Pan-American Highway at the eastern edge of the Plains of Tehuantepec; dense scrub forest [47]. Most collections were made in the scrub forest 5 to 8 kilometers west-northwest of the village.

Zarzamora.—Lat. 16° 21′; long. 95° 48′; elev. 800 m. A ranch between La Reforma (16 kilometers west of Tequisistlán) and Santa María Ecatepec; scrub forest with oaks on higher ridges [59].

Veracruz

Acayucan.—Lat. 17° 57′; long. 94° 55′; elev. 160 m. A large town on the Trans-isthmian Highway; rainforest [21]. Collections were made in the vicinity of the town, but principally at Rancho Las Hojitas, 7 kilometers northwest of town at an elevation of 150 meters.

Alvarado.—Lat. 18° 47′; long. 95° 47′; sea level. A fishing village at the mouth of the Río Papaloapan; coastal dunes and marshes [1]. Most collections were made 1-3 kilometers southeast of the village in marshes on the leeward side of the coastal dunes.

Amatitlán.—Lat. 18° 26′; long. 95° 45′; elev. 4 m. A village on the bank of the Río Papaloapan; savanna and sugar plantations [6].

Aquilera.—Lat. 17° 48′; long. 95° 01′; elev. 150 m. A village 21 kilometers southwest of Acayucan on the Trans-isthmian Highway; rainforest [22].

Ayentes.—Lat. 18° 10′; long. 94° 26′; elev. 2 m. A railroad station on the east bank of the Río Coatzacoalcos, across the river from the city of Coatzacoalcos; scrub forest and marshes [17].

Berta.—Lat. 18° 07′; long. 94° 27′; elev. 5 m. A ranch just south of Coatzacoalcos; scrub and low evergreen forest [15].

Chacaltianguis.—Lat. 18° 18′; long. 95° 52′; elev. 5 m. A village on the Río Papaloapan; savanna [8].

Ciudad Alemán.—Lat. 18° 13′; long. 96° 07′; elev. 30 m. A new government town, headquarters of the Comisión del Papaloapan; scrub and low evergreen forest [10].

Coatzacoalcos (formerly Puerto México).—Lat. 18° 10′; long. 94° 27′; elev. 2 m. A seaport at the mouth of the Río Coatzacoalcos; scrub on coastal dunes; marshes and low evergreen forest inland [16]. Most collections are from the forest-savanna ecotone, 8 kilometers southwest of town.

Cosamaloapan.—Lat. 18° 22′; long. 95° 50′; elev. 4 m. An agricultural town on the Río Papaloapan; savanna and sugar plantations [7].

Cosoleacaque.—Lat. 17° 59′; long. 94° 38′; elev. 55 m. A village 8 kilometers by road west of Minatitlán; savanna [19].

Cuatotolapam.—Lat. 18° 08′; long. 95° 16′; elev. 13 m. A village on the Trans-isthmian Railroad; savanna and low evergreen forest along streams [13].

Hueyapan.—Lat. 18° 08′; long. 19° 09′; elev. 85 m. A town 32 kilometers by road northwest of Acayucan; savanna and low evergreen forest [14]. Collections were made in the vicinity of the town and from forest 10 kilometers southeast of town at an elevation of 135 meters.

Jesús Carranza (formerly Santa Lucrecia).—Lat. 17° 27′; long. 95° 02′; elev. 80 m. A town and railroad junction in the middle of the isthmus; rainforest [26]. Most of Dalquest's specimens came from varying distances from Jesús Carranza along the Río Coatzacoalcos and its tributaries.

Minatitlán.—Lat. 17° 58′; long. 94° 32′; elev. 15 m. An oil refinery center on the Río Coatzacoalcos; savanna [20].

Naranjo.—Lat. 17° 35′; long. 95° 07′; elev. 100 m. A village on the Trans-isthmian Highway, 45 kilometers south of Acayucan; rainforest and palm forest [24].

Novillero.—Lat. 18° 16′; long. 95° 59′; elev. 10 m. A village on the Río Papaloapan; scrub forest and grassland [9].

Oaxaqueña, La.—Lat. 17° 26′; long. 94° 53′; elev. 80 m. A hacienda on the Río Coatzacoalcos about 12 kilometers east of Jesús Carranza; rainforest [27].

Playas, Río de las.—Lat. 18° 08′; long. 94° 07′; elev. 3 m. The river (sometimes known as the Río Tonolá) forming the boundary between the states of Veracruz and Tabasco; rainforest [18].

San Lorenzo.—Lat. 17° 44′; long. 94° 42′; elev. 25 m. A village on the Río Chiquito, about 30 kilometers southeast of Acayucan; rainforest [23].

Suchil.—Lat. 17° 31′; long. 95° 03′; elev. 40 m. A village on the Trans-isthmian Railroad, about 10 kilometers north of Jesús Carranza; rainforest [25].

Tecolapan.—Lat. 18° 24′; long. 95° 18′; elev. 275 m. A village on a small river of the same name in the western foothills of Los Tuxtlas; rainforest [5].

Tejada, Lerdo de.—Lat. 18° 37′; long. 95° 31′; elev. 60 m. An agricultural village, 35 kilometers by road east-southeast of Alvarado; scrub forest, marshes, and sugar plantations [2]. Collections were made in a marsh, 5 kilometers west-northwest of the village.

Tlacotalpan.—Lat. 18° 37′; long. 95° 42′; elev. 3 m. A town at the confluence of the Río San Juan and Río Papaloapan; marshes and sugar plantations [3].

Tula.—Lat. 18° 36′; long. 95° 22′; elev. 150 m. A village near the western base of Los Tuxtlas; low evergreen forest and marshes [4]. Collections were made in a marsh 3 kilometers northwest of the village.

THE AMPHIBIAN FAUNA OF THE LOWLANDS

In presenting an account of the amphibian fauna of the lowlands of the Isthmus of Tehuantepec three items must be considered:

1. The composition of the fauna.
2. The ecology of the fauna.
3. The distribution of the fauna.

These items, together with similar data concerning the amphibians of the adjacent highlands, will form the basis for the subsequent discussion of the establishment of present patterns of distribution in the isthmian region.

Composition of the Fauna

The amphibian fauna of the lowlands of the Isthmus of Tehuantepec consists of 36 species definitely recorded from the area. These include one genus and species of caecilian, one genus, including three species of salamanders, and 14 genera and 32 species of anurans.

In comparison with the known amphibian fauna of the forested and savanna portions of El Petén, Guatemala (Stuart, 1935 and 1958), we find that there are more species recorded from the isthmus than from El Petén. Stuart found only 20 species of amphibians in both forest and savanna habitats in El Petén. Of the 36 species of amphibians known from the isthmus, 28 occur on the Gulf lowlands and live in forest or savanna habitats.

The geographic position of the isthmus with regard to major faunal areas in Middle America, and the diversity of the environment are important factors in understanding the presence of a large number of species of amphibians in the isthmus. The large number of species probably is a reflection of the diversity of the environment; this diversity is the result of fluctuation of climate, and thus environments, in the not too distant past. In no individual habitat, such as rainforest, savanna, or scrub forest, does the number of species approach the total for the region.

Ecology of the Fauna

In the preceding section on the description of the Isthmus of Tehuantepec I have outlined the major environments in the region. With respect to the distribution of amphibians we may recognize three major environments in the isthmus—rainforest, semi-arid scrub forest, and savanna. Each of these has varying combinations of physical and biotic factors that are important in the ecology of amphibians. Because of the importance of moisture, not only for the maintenance of life in these animals, but in most species their dependence on water for breeding purposes, this environmental factor is considered the most significant in the ecological distribution of amphibians. A second factor is the availability of necessary shelter, especially aestivation sites. These factors will be compared in the three major environments in the region.

Moisture is present in the environment in the form of free water or atmospheric moisture. With respect to the latter, it is well known that dense shaded forests have a considerably higher relative humidity than do open plains or areas with only scattered trees. Thus, the rainforests of the isthmus are characterized by a much higher relative humidity than are the savannas or semi-arid scrub forests. Although with regard to rainfall there is a pronounced dry season in the regions supporting rainforest, there still remains considerable atmospheric moisture in this environment throughout the year. The dense foliage provides shade and protection from desiccating effects of wind and sunlight; furthermore the foliage contributes moisture by transpiration. The deep alluvial soils mixed with large quantities of organic matter (decaying leaves and rotting logs) maintain considerable quantities of moisture.

Conversely, the savannas and scrub forests have little atmospheric moisture during the dry season. In the former habitat there are few trees to provide shade or moisture through transpiration; in the latter most of the trees lose their leaves during the dry season. Thus, these environments are desiccated by the dry winds and direct sunlight. Furthermore, the soils in these environments become dry and caked. There is little or no terrestrial matter to hold moisture.

Free water in these environments is present in a variety of forms at different times of the year. During the dry season the more extensive marshes in the savannas persist; many ponds and most of the streams in the rainforest are permanent throughout the year. In the scrub forest all except the largest streams become dry during the dry season, and no ponds exist through the dry season. With the advent of the first heavy summer rains the stream beds fill with water, marshes expand, and many depressions become ponds (Pl. 5, fig. 2). At this time the amount of free water in the scrub forests and savannas greatly increases, much more so than that in the rainforests.

Environments are vertically stratified in the rainforests. There is the deep alluvial soil, the ground litter of leaves and decaying logs, the low bushes and small trees, and finally the tall trees of the forest. Each of these provides certain types of shelter for amphibians. The moist soil and litter on the forest floor is an important microhabitat for fossorial and strictly terrestrial species. The dense foliage of the trees, tree holes, and bromeliads growing on the trees provide shelter for arboreal species. Arboreal and terrestrial bromeliads and the terrestrial elephant-ear plants (*Xanthosoma*) contain water in the axils of their leaves throughout the year and thus provide an important habitat for amphibians. The low, spiny, deciduous trees of the scrub forest and the grasses and scattered trees in the savannas provide little shelter. In the savannas there are depressions, some of which contain water throughout the year; these are often surrounded by trees providing refugia for amphibians during the dry season. In the scrub forest many species congregate along streams and in moist stream beds during the dry season.

Now that the important ecological factors of the major environments have been outlined, we may examine the local distribution of amphibians in each of these. Beginning with the rainforest, we find only one fossorial species, *Gymnopis mexicanus.* A large number of species are found on the forest floor; characteristic inhabitants of the leaf litter are: *Bufo valliceps, Eleutherodactylus rhodopis, Microbatrachylus pygmaeus,* and *Syrrhophus leprus.* Other terrestrial amphibians usually are not scattered throughout the rainforest, as are those named immediately above, but instead inhabit areas of forest adjacent to ponds or streams; these species include: *Bufo marinus, Eleutherodactylus natator, Eleutherodactylus rugulosus, Leptodactylus labialis, Leptodactylus melanonotus, Rana palmipes* and *Rana pipiens.* The most striking ecological assemblage of amphibians in the rainforest is the arboreal group of species, including:

Bolitoglossa occidentalis
Bolitoglossa platydactyla
Eleutherodactylus alfredi
Hyla baudini
Hyla ebraccata
Hyla loquax
Hyla microcephala martini
Hyla picta
Phrynohyas modesta
Phrynohyas spilomma
Phyllomedusa callidryas taylori

In the savannas *Rhinophrynus dorsalis, Engystomops pustulosus,* and *Gastrophryne usta* are fossorial species. *Bufo marinus, Leptodactylus melanonotus, Leptodactylus labialis, Rana palmipes,* and *Rana pipiens* are found in the vicinity of permanent water in the savannas. Although the savanna habitat does not provide the ecological conditions for the existence of an arboreal fauna, many arboreal species from the surrounding rainforest utilize the extensive marshes and ponds in the savannas for breeding purposes. Thus, *Hyla baudini, Hyla microcephala martini, Hyla picta,* and *Phrynohyas spilomma* have been found breeding in savannas. In parts of savannas where clumps of trees surround depressions containing water throughout the year, individuals of the species named above, together with *Hyla loquax* and *Phyllomedusa callidryas taylori,* may not only breed, but remain throughout the year.

In the semi-arid scrub forest the same fossorial species as exist in the savannas are found. Likewise, *Bufo marinus, Leptodactylus labialis, Leptodactylus melanonotus,* and *Rana pipiens* are found near permanent water. Terrestrial species in this semi-arid environment include *Bufo canaliferus, Bufo coccifer, Bufo marmoreus, Syrrhophus pipilans,* and *Diaglena reticulata.* Of these, *Syrrhophus pipilans* sometimes inhabits low trees and bushes; the others may be fossorial. The arboreal species in the scrub forest include *Hyla baudini, Hyla robertmertensi, Hyla staufferi,* and *Phyllomedusa dacnicolor.*

Eleutherodactylus rugulosus and *Hylella sumichrasti* live along streams in the scrub forest. *Hylella sumichrasti* lays its eggs in these streams.

In comparing the ecological differences in the amphibian assemblages in the three major habitats, the most obvious difference is the great percentage of arboreal species in the rainforest as compared with savanna and scrub forest. Only four arboreal species are found in the scrub forest, none in the savannas, but eleven in the rainforest. Likewise, there is an absence of ground-dwelling forms in the arid habitats; in the latter the only terrestrial species are those that are found near water. A possible exception is *Syrrhophus pipilans.*

From the above analysis of ecological distribution we may see that the rainforest provides a variety of habitats for amphibians and that these habitats are suitable for amphibian life throughout the year. On the other hand, the savannas and scrub forests are characterized by extreme conditions of desiccation, a factor of considerable importance in limiting the ecological distribution of amphibians. However, there still is a diversity of amphibians in these semi-arid environments. Obviously, these species are adapted in various ways for survival during the dry season, at which time environmental conditions are such that the animals cannot carry on their normal activities.

Although there is not an abundance of data concerning the seasonal activity of the fauna, what is available shows some interesting correlations with the environments. During the dry season in the scrub forest there is essentially no amphibian activity; an occasional *Rana pipiens* may be seen along a river, or a *Bufo marinus* may be seen at night. In the rainforest the terrestrial-breeding amphibians are active during the dry season. *Eleutherodactylus rugulosus* is found at night or by day along streams. *Eleutherodactylus rhodopis, Microbatrachylus pygmaeus,* and *Bufo valliceps* are active during the day; these plus *Bolitoglossa occidentalis, Bolitoglossa platydactyla, Eleutherodactylus alfredi, Eleutherodactylus natator,* and an occasional *Hyla* are active at night.

With the onset of the heavy summer rains and the subsequent formation of breeding ponds, amphibian activity reaches a peak. This is especially noticeable in the semi-arid environments, where during the dry season there is little activity.

Among the anurans in the isthmus the four species of *Eleutherodactylus,* the two species of *Syrrhophus,* and the one species of *Microbatrachylus* are either known, or presumed, to lay eggs on the ground; these develop directly into small frogs. All of the other anurans deposit their eggs in water or attach them to objects over water (*Phyllomedusa*); these hatch into tadpoles, which later metamorphose into frogs. *Hylella sumichrasti* is known to breed only in streams. All of the other species breed in ponds, but at times some species deposit their eggs in streams; in this last group are *Bufo valliceps, Bufo marmoreus, Phyllomedusa callidryas taylori,* and *Rana pipiens.*

Although the ecological data are incomplete, they do show that ecological conditions differ greatly in the three major environments, different species of amphibians inhabit these environments, and that the fauna is ecologically diversified in each environment.

Distribution of the Fauna

Plotting the distributions of species of amphibians known to live in the lowlands of the Isthmus of Tehuantepec results in an array of geographic patterns. These may be analyzed with respect to those species that are restricted either to the Gulf lowlands or the Pacific lowlands, or those that occur on both the Gulf and Pacific lowlands. Furthermore, the distributions may be analyzed with respect to those species whose ranges extend from México across the Isthmus of Tehuantepec into Central America, those that reach the isthmus from Central America but do not extend into México proper, and those that reach the isthmus from México but do not extend into Central America. It should be kept in mind that the following analysis is of the lowland inhabitants only. Species inhabiting the foothills and mountains will be discussed later.

1. SPECIES RESTRICTED TO THE GULF LOWLANDS. Of the 36 species of amphibians recorded from the Isthmus of Tehuantepec, nine (25 per cent) are in this group. Four of these (*Eleutherodactylus alfredi, Syrrhophus leprus, Hyla loquax,* and *Hyla picta*) live in the Gulf lowlands to the east and to the west of the isthmus. Three others (*Hyla ebraccata, Hyla microcephala martini* and *Phyllomedusa callidryas taylori*) are primarily Central American in their distribution and reach the northwestern limits of their ranges in the Gulf lowlands of the isthmus, whereas *Bolitoglossa platydactyla* and *Eleutherodactylus natator* reach the southern limits of their distributions in the isthmus.

2. SPECIES RESTRICTED TO THE PACIFIC LOWLANDS. This group includes six species, or 17 per cent of the amphibian fauna of the isthmus. Two of these (*Bufo coccifer* and *Syrrhophus pipilans*) range to the east and to the west of the isthmus on the Pacific lowlands. Two others (*Bufo canaliferus* and *Hyla robertmertensi*) range from the isthmus into Central America, and *Diaglena reticulata* and *Phyllomedusa dacnicolor* range on the Pacific lowlands of México southeastward to the isthmus.

3. SPECIES THAT OCCUR ON THE PACIFIC AND GULF LOWLANDS. This group includes 19 species, or 53 per cent of the total amphibian fauna. Of these, nine species (25 per cent of the entire amphibian

fauna) are widespread throughout the lowlands of México and Central America; these are:

Gymnopis mexicanus
Rhinophrynus dorsalis
Bufo marinus
Engystomops pustulosus
Leptodactylus labialis
Leptodactylus melanonotus
Hyla baudini
Hyla staufferi
Rana pipiens

Four species occur on the Gulf lowlands to the east and to the west of the isthmus, but on the Pacific lowlands they occur only to the east; this group includes *Bufo valliceps, Eleutherodactylus rhodopis, Phrynohyas modesta,* and *Phrynohyas spilomma.* Three species live to the east and to the west of the isthmus on the Pacific lowlands, but only to the west on the Gulf lowlands; these include *Eleutherodactylus rugulosus, Microbatrachylus pygmaeus,* and *Gastrophryne usta.*

Six species that cross the isthmus live on the humid Gulf lowlands and on the humid lowlands of Chiapas and Guatemala, but not on the semi-arid Plains of Tehuantepec; these include *Bolitoglossa occidentalis, Eleutherodactylus rhodopis, Microbatrachylus pygmaeus, Phrynohyas modesta, Phrynohyas spilomma,* and *Rana palmipes.* Of these, *Microbatrachylus pygmaeus* also occurs in scattered humid environments to the west of the isthmus on the Pacific lowlands.

Two species are endemic to the isthmian region. *Bolitoglossa veracrucis* is known only from the humid northern slopes of the isthmus. *Hylella sumichrasti* occurs on the Pacific slopes of the isthmus and extends to the east into western Chiapas.

In analyzing the distribution of the amphibians with respect to those that are restricted to either the Pacific or Gulf lowlands or those that cross the continental divide in the isthmus, we find that 25 per cent of the species are restricted to the Gulf lowlands, 17 per cent are restricted to the Pacific lowlands, and 53 per cent cross the isthmus. In analyzing the distribution patterns with respect to those that extend across the isthmus of Tehuantepec from east to west, we find that 14 per cent of the species do not extend east of the isthmus into Central America and that 19 per cent do not range west of the isthmus into México proper; 61 per cent of the species range to the east and to the west of the isthmus. Of the 36 species of amphibians inhabiting the isthmus only nine species (25 per cent) range across the isthmus, that is, occur on the Gulf and Pacific lowlands, and also range to the east and to the west of the isthmus. To these wide-ranging species the diversified environments of the isthmus do not present a barrier to distribution. The other 27 species (75 per cent) either do not cross the isthmus from east to west or from north to south; thus, probably in one way or another the isthmus presents a barrier to their distribution.

THE AMPHIBIAN FAUNA OF THE FOOTHILLS AND ADJACENT HIGHLANDS

To amphibians inhabiting the foothills and mountains of southern México and northern Central America, the isthmus presents a great barrier to dispersal. For example, salamanders of the genus *Thorius,* the *mexicanus* and *augusti* groups of the genus *Eleutherodactylus,* the *bistincta* group of the genus *Hyla,* and the genus *Tomodactylus* occur on the Mexican Plateau and southward into the mountains of Oaxaca. Nevertheless, no members of these groups are present in the Guatemalan-Chiapan Highlands. The genera *Chiropterotriton, Magnadigita, Pseudoeurycea,* and *Ptychohyla*, as well as the *eximia* group of *Hyla* are represented by different species in the Guatemalan-Chiapan Highlands than in the mountains of México on the other side of the isthmus. Several species of *Plectrohyla* occur in the Guatemalan-Chiapan Highlands, but none is known from the Mexican Highlands, although one species occurs in the Tuxtlas.

Living in the humid forests of the foothills are salamanders of the genus *Lineatriton,* frogs of the *spatulatus* group of *Eleutherodactylus, Anotheca coronata, Hyla miotympanum,* and *Phyllomedusa moreleti.* All of these occur in the foothills of the Sierra Madre Oriental in eastern México and in Los Tuxtlas. *Lineatriton, Hyla miotympanum,* and the *spatulatus* group of *Eleutherodactylus* do not occur in the foothills of the Guatemalan-Chiapan Highlands; those amphibians reach the end of their ranges at the isthmus. *Phyllomedusa moreleti* and *Anotheca coronata* are found in the northern foothills of the Guatemalan-Chiapan Highlands, and *Phyllomedusa moreleti* is found in the foothills on the Pacific slopes of the Chiapan Highlands.

Although the above analysis is not so detailed as that of the lowland inhabitants, it does show that all of the genera and species of amphibians known to inhabit the foothills and highlands adjacent to the isthmus, only two species of amphibians cross the isthmus from one highland mass to the other. Thus, it is evident that the Isthmus of Tehuantepec presents a great barrier to dispersal of these groups of amphibians.

ESTABLISHMENT OF PRESENT PATTERNS OF DISTRIBUTION

From the foregoing analysis of geographical and ecological distribution in the Isthmus of Tehuantepec we may strive for an interpretation of the events that led to the establishment of patterns of distribution displayed not only by the amphibians, but other terrestrial vertebrates as well. The thesis that I am proposing below is based on the premise that in southern México and northern Central America climatic fluctuation during the Pleistocene was of sufficient magnitude to cause vegetational shifts, both vertically and latitudinally, resulting in the establishment of alternating continuous and discontinuous lowland and highland environments, although this climatic fluctuation was not so great as to eliminate tropical lowland environments from the region. I feel that the present patterns of distribution of the amphibians in the Isthmus of Tehuantepec may be explained on this premise.

Many authors dealing with the herpetofauna of Middle America have followed Schuchert's (1935) suggestion of a seaway in the isthmus during the Cenozoic. Thus, Burt (1931), Duellman (1956, 1958a), Gloyd (1940), Oliver (1948), Smith and Laufe (1946), and Stuart (1941) employed the presence of a seaway to explain distribution and speciation in various genera. Durham, Arellano, and Peck (1952), Olson and McGrew (1941), and Stirton (1954) have provided geological evidence that there probably was no Cenozoic seaway in the Isthmus of Tehuantepec. Even if there were a seaway in the Pliocene or Miocene (the dating of this possible seaway is open to question), its presence is not necessary to explain the present patterns of distribution in the isthmus.

In recent years the study of natural biotic environments, palynology, and Pleistocene chronology in Middle America has produced a wealth of data, which although still fragmentary begins to form a picture of past climatic events in that part of the world. Sedimentary studies by Hutchinson, Patrick, and Deevey (1956) and Sears, Foreman, and Clisby (1955) have provided evidence of drastic climatic shifts in México during the Pleistocene. Further evidence of bioclimatic fluctuation is provided by Martin and Harrell (1957) and Martin (1958); the latter has suggested that there was a displacement of the tropical zones in southern México and northern Central America by as much as 3000 feet during the glacial maximum. Much of the evidence of such drastic vertical shifts in environments is based on the presence of Pleistocene montane glaciers on Mexican volcanoes (White, 1956) and Chirripo in Costa Rica (Weyl, 1955). Dorf (1959) supports this idea of drastic climatic change.

In his studies of the avifauna of México and Guatemala Griscom (1932 and 1950) made an important issue of the continuity of the bird fauna in what he called the Subtropical Life-zone, which essentially consists of cloud forest, a widespread, but discontinuous, habitat on the Gulf (windward) slopes of the Mexican and Central American highlands at elevations between 1000 and 2000 meters. To account for this apparent uniformity in the avifauna Griscom hypothesized a continuity of cloud forest environment in the Pleistocene; this would result in the depression of cloud forests to the coastal lowlands and the displacement of tropical lowland environments far to the south in Central America. Stuart (1951) objected to this displacement of lowland tropical rainforest; he stated that a descent to sea level of a subtropical zone would have brought about either widespread extermination of the tropical fauna or acclimatization of that fauna to subtropical conditions.

Although palynological studies and some faunal studies of subtropical and temperate animals suggest a drastic climatic fluctuation that might have eliminated tropical environments in southern México and northern Central America, there is much biological evidence indicating the existence of tropical environments in this region even during the glacial maximum. Especially significant is the diversity of species inhabiting the present tropical environments; many of these have differentiated from related taxa to the south.

In the Pleistocene, climate fluctuated and vegetation shifted correspondingly in southern México and northern Central America. Most of the palynological studies and many studies of Pleistocene chronology deal with montane regions, either the Mexican Plateau or the mountains rising from the plateau. No such studies have been made in lowland tropical environments. During glacial advances the tropical lowland environments in México probably were not eliminated, for the great diversity of animals in these environments supports the hypothesis that they have been in existence for some time, although periodically they may have been discontinuous.

In order to understand the nature of bioclimatological events in the Pleistocene in lowland tropical environments of southern México, certain factors that are of little importance in the interpretation of Pleistocene chronology in the highlands must be considered. These factors are: 1) climatic moderation by oceans, 2) fluctuation in sea level, and 3) fluctuation in level of the water table as affected by sea level.

It is well-known that large bodies of water moderate the temperature on adjacent land. Furthermore, it is kown that faunas of marine invertebrates shifted latitudinally in the Pleistocene; Trask, Phleger, and Stetson (1947) recorded cold-water Foraminifera then as far south as the Sigsbee Deep in the middle of the Gulf of Mexico. Large bodies of warm water, such as the Gulf of Mexico, Caribbean Sea, and Pacific Ocean of today, probably were not sufficiently cooled at the time of glacial advance to affect greatly the temperature of the winds blowing across them. Even if these bodies of water were somewhat cooler than now, the prevailing winds blowing from them onto the lowlands of México and northern Central America would have aided in maintaining relatively high temperatures there. These warm winds probably counteracted the cooling effect of glaciation in the lowlands and thereby maintained tropical conditions near the seas.

Although no adequate studies of Pleistocene beach lines have been made in southern México, such information is available for peninsular Florida on the other side of the Gulf of Mexico (Cooke, 1945). Fluctuation in sea level in the Pleistocene has been used by Hubbell (1954), Goin (1958), and Duellman and Schwartz (1958) to explain present patterns of distribution of animals in Florida. If Cooke's interpretations can be applied to the western side of the Gulf of Mexico, even generally, it would be supposed that sea level varied from about 300 feet lower than at present during the Illinoian Glacial Period to about 275 feet higher than at present during the Aftonian Interglacial Period. Lowering of sea level would expand the lowlands in the isthmus; rising sea level would restrict them, leaving only the central ridges and many islands in the isthmus, but never forming a seaway between the Gulf of Mexico and the Pacific Ocean.

Probably the level of the water table in the coastal lowlands and the gradients of the streams in the lowlands and foothills was closely correlated with fluctuation in sea level. If sea level fluctuated as much as 575 feet in the Pleistocene, changes in the level of the water table must have been of considerable magnitude.

During times of glacial advances the lowlands of the isthmus probably were more extensive and had more semi-arid tropical environments than at present, with patches of rainforest existing in sheltered valleys along the major streams. In the course of bioclimatic fluctuation the semi-arid environments (scrub forest and/or savanna) were continuous at times from the Pacific lowlands across the isthmus to the Gulf lowlands. At those times such typical inhabitants of the semi-arid environments as *Rhinophrynus dorsalis, Engystomops pustulosus,* and *Hyla staufferi* could have made their way across the isthmus. At times of most extensive glaciation, such as the Illinoian, temperatures in the isthmus probably were low enough to permit the growth of pine-oak forest and cloud forest continuously across the central ridges from the Mexican to the Chiapan-Guatemalan highlands. At those times such highland members of the fauna as *Chiropterotriton, Pseudoeurycea, Magnadigita,* and the *eximia* group of *Hyla* could have crossed the isthmus. During Wisconsin time, climate probably fluctuated less than during previous glaciations; probably no montane environments, except cloud forest, were represented in the isthmus during the Wisconsin. Even at this relatively late date such animals as *Lineatriton lineola, Anotheca coronata,* and *Phyllomedusa moreleti* could have crossed the isthmus.

During the interglacial periods, which in the isthmian region were characterized by warmer temperatures, higher sea level and consequently more restricted areas of lowlands, and possibly more rainfall than in the glacial periods, the continuity of pine-oak forest and cloud forest from east to west across the isthmus was interrupted. Probably, too, the semi-arid environments were restricted, and the rainforests were more widespread. At those times animals now inhabiting the rainforests of the Gulf lowlands and those inhabiting the Pacific lowlands of Chiapas and Guatemala could have crossed the isthmus. In this group are species such as *Bolitoglossa occidentalis, Eleutherodactylus rhodopis, Microbatrachylus pygmaeus,* and *Rana palmipes.*

The amount of differentiation in isolated populations of amphibians in southern México and northern Central America gives some idea of relative lengths of time of isolation from related populations. Those populations inhabiting high mountain environments on either side of the isthmus are specifically distinct. Some populations inhabiting cloud forests lower on the mountains are specifically distinct from related populations on the other side of the isthmus; between others there is no recognizable differentiation. Even though many populations are isolated from other populations of the same species in the lowlands of the isthmus, there is no apparent speciation. This indicates that the lowland environments and their inhabitants have been isolated from one another for a shorter time than have the highland environments and their inhabitants.

ACCOUNTS OF SPECIES

For each species of amphibian known to occur in the lowlands of the Isthmus of Tehuantepec, localities where one or more specimens were collected are listed, and variation, ecology, and life histories are discussed. A total of 2833 specimens has been examined for the purposes of this study. Individual specimens cited in the text are listed with catalogue numbers and abbreviations of the name of the museum, as follows:

AMNH	American Museum of Natural History
KU	University of Kansas Museum of Natural History
MCZ	Museum of Comparative Zoology, Harvard College
UIMNH	University of Illinois Museum of Natural History
UMMZ	University of Michigan Museum of Zoology
USNM	United States National Museum

Gymnopis mexicanus mexicanus Duméril and Bibron

Oaxaca: El Barrio (3); Matías Romero; Tehuantepec (2). *Veracruz:* Cosamaloapan; Cuatotolapam (2).

The two specimens from Cuatotolapam were collected by Ruthven in an area of mixed savanna and forest. The three specimens (USNM 30535-7) listed above from El Barrio were collected by Sumichrast; possibly they came from another locality. The city of Tehuantepec is divided into seven districts called "barrios." The two specimens listed from Tehuantepec (MCZ 1604) merely bear the data "Tehuantepec, Mexico." They may have come from the town, the district, or from anywhere in the isthmus. The specimen from Matías Romero has 109 primary and 67 secondary annuli, a length of 400 mm., and a diameter of 19 mm.; the one from Cosamaloapan has 106 primary and 58 secondary annuli, a length of 397 mm., and a diameter of 19 mm. Data on the other specimens were recorded by Dunn (1942:475).

Bolitoglossa occidentalis Taylor

Oaxaca: Río Sarabia (2); Ubero. *Veracruz:* La Oaxaqueña; 14 km. E of Suchil.

The specimens from Oaxaca are only tentatively assigned to *occidentalis.* All are immature and lack maxillary teeth. Taylor (1941:147) stated that the maxillary teeth are absent in young *occidentalis.* One from Río Sarabia is a male with a body-length of 29 mm. and a tail-length of 22 mm. The dorsum is reddish brown streaked with dark gray; the venter is dark gray. Two small individuals (one from Sarabia and one from Ubero) have body-lengths of 19 and 21 mm. and tail-lengths of 10.5 and 11 mm. In life they were pale yellowish tan above with a brown triangular mark on the occiput, but with no middorsal stripe. Both were found in the axills of elephant ear plants (*Xanthosoma*).

This species has been noted by Goodnight and Goodnight (1956: 146) on the Atlantic lowlands at Palenque, Chiapas, and by Shannon and Werler (1955:362) at several localities in Los Tuxtlas, Veracruz. I have collected it at Vista Hermosa on the eastern slopes of the Sierra Madre Oriental above Tuxtepec in northern Oaxaca. Both *B. occidentalis* and *B. rufescens* have been reported from Palenque, Chiapas (Taylor and Smith, 1945:547). Reëxamination of specimens from northern Chiapas and Tabasco is needed to verify the sympatric occurrence of these two similar species.

Bolitoglossa platydactyla Tschudi

Oaxaca: La Oaxaqueña; Tolosita (2). *Veracruz:* Acayucan; Cuatotolapam; 25 km. ESE of Jesús Carranza; 14 km. E of Suchil; 2.7 km. N of Tula.

Known only from the Gulf lowlands in the isthmian region, this species has been taken in a variety of habitats within the humid forest area: under outer leaves of banana plants, under a rock along a stream, under a log in a plowed field, and on a reed in a pond at night. Three adult males have an average snout-vent length of 44 mm. and a tail-length of 41 mm. In life the color of the dorsum varied from orange-yellow to orange-tan, usually being more orange on the tail. The iris was a reddish orange.

Bolitoglossa veracrucis Taylor

Veracruz: 35 km. SE of Jesús Carranza (21).

This species is known only from the type series collected at night on a limestone cliff by Walter W. Dalquest. If this salamander is restricted to this type of habitat, it should be found in the region of extensive limestone outcroppings in northern Chiapas and southern Tabasco.

Rhinophrynus dorsalis Duméril and Bibron

Oaxaca: Ixtepec; Limón; Salina Cruz (18); Tehuantepec (57); Tuxtepec (3). *Veracruz:* Amatitlán (3); Cosamaloapan (5); Novillero (2); San Lorenzo.

This species inhabits the scrub forests of the Pacific coastal plain and the savannas in southern Veracruz; apparently it does not occur in rainforest. Consequently, its distribution in the isthmus is discontinuous.

PLATE 1

Fig. 1. Savanna about 75 kilometers east of Coatzacoalcos, Veracruz. Photograph by L. C. Stuart.

Fig. 2. Low scrub forest near Alvarado, Veracuz. Photograph by L. C. Stuart.

PLATE 2

FIG. 1. Rainforest near Tolosita, Oaxaca. March, 1956.

FIG. 2. Rainforest along the Río Sarabia, Oaxaca. March, 1956.

PLATE 3

FIG. 1. Transition forest near La Princesa, Oaxaca. March, 1956.

FIG. 2. Palm Savanna on the Plains of Chivela, Oaxaca. March, 1956.

PLATE 4

Fig. 1. Scrub forest on the Plains of Tehuantepec in dry season. March, 1956.

Fig. 2. Scrub forest on the Plains of Tehuantepec in rainy season. View toward the north. In the distance is the Continental Divide in the hills of the Isthmus. July, 1958.

PLATE 5

FIG. 1. Low, dense scrub forest near La Ventosa, Oaxaca. July, 1958.

FIG. 2. Temporary pond in scrub forest north of Salina Cruz, Oaxaca. July 7, 1958. *Rhinophrynus dorsalis, Bufo marmoreus*, and *Diaglena reticulata* were breeding here the previous night.

PLATE 6

FIG. 1. Calling male of *Rhinophrynus dorsalis*, photographed in a pond north of Santa Cruz, Oaxaca, on July 6, 1958. × ⅔.

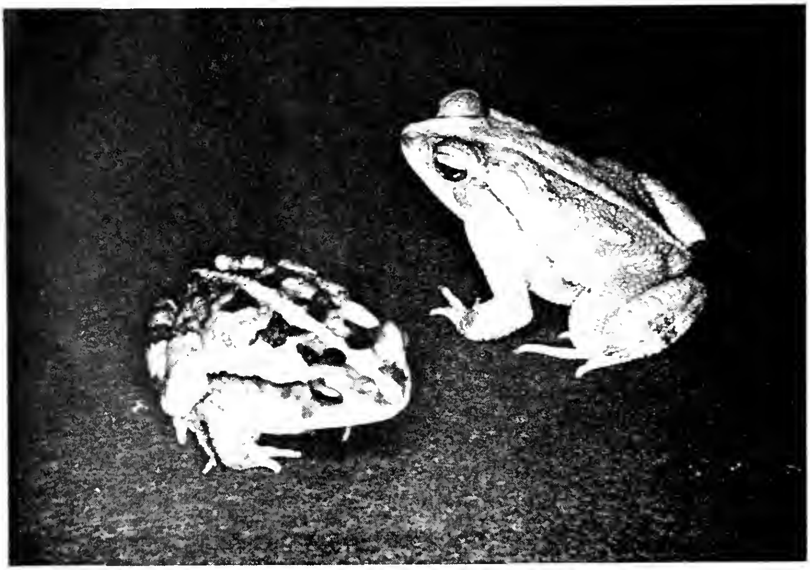

FIG. 2. Color pattern variation in two adults of *Bufo canaliferus* from Juchitán, Oaxaca. × ⅔.

FIG. 1. Calling male of *Engystomops pustulosus*, photographed in a pond west of Tehuantepec, Oaxaca, on July 5, 1956. × 2.

FIG. 2. Foamy egg mass of *Engystomops pustulosus* at the edge of a pond west of Tehuantepec, Oaxaca. July 5, 1956. × ⅜.

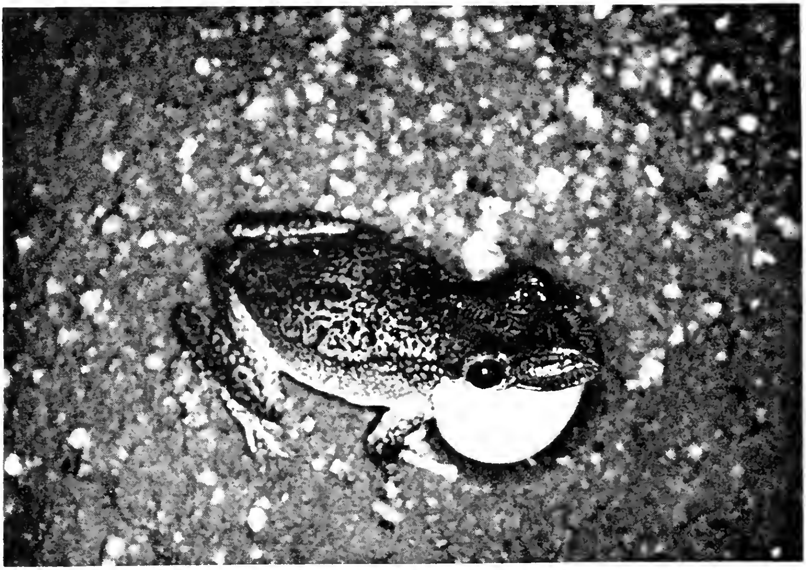

FIG. 1. Calling male of *Diaglena reticulata*, photographed at a pond north of Salina Cruz, Oaxaca, on July 6, 1958. × ½.

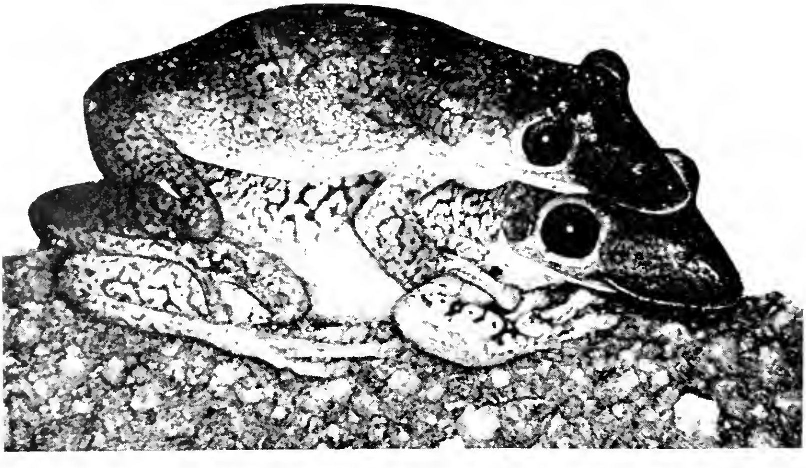

FIG. 2. Clasping pair of *Diaglena reticulata* at the edge of a pond north of Salina Cruz, Oaxaca, on July 6, 1958. × 1.

Breeding congregations were found after heavy rains at Tehuantepec on July 5, 1956, at Cosamaloapan, Novillero, and Amatitlán on July 26, 1956, and at Salina Cruz on July 6, 1958. The call is a long "worrp" made while the male is floating on the surface of the pond. The small heads, small limbs, and greatly inflated bodies cause the calling males to resemble miniature caricature balloons (Pl. 6, fig. 1). Amplexus is inguinal. These toads are notably wary, even when calling. Often the beam of a flashlight or the slightest disturbance of the water will cause the males to stop calling. The body is deflated with one last nauseous note, and the frog sinks beneath the surface of the water and swims away with short slow kicks of the hind feet.

Bufo canaliferus Cope

Oaxaca: Chivela; Salina Cruz; Santa Efigenia; Tapanatepec (6); Tehuantepec (10); Zanatepec (4).

This small toad apparently is restricted to the Pacific lowlands from the Isthmus of Tehuantepec eastward to Guatemala. At Zanatepec on July 13, 1956, males were calling from a flooded field bordered by scrub forest. The call is a rather loud nasal racket. Living individuals vary greatly in coloration. Some have yellowish tan flanks and dorsum and an orange middorsal stripe; others have a pale red dorsum, yellow flanks, and a cream middorsal stripe (Pl. 6, fig. 2).

Bufo coccifer Cope

Oaxaca: Juchitán (5); Tehuantepec.

It is with some degree of hesitancy that these toads are referred to the species *coccifer.* Although these and other specimens from Guerrero and Michoacán display no striking differences from specimens from Costa Rica, Nicaragua, and southeastern Guatemala, the ranges of the populations are separated by a broad hiatus in Chiapas and Guatemala. Possibly this species has utilized the sub-humid corridor through northern Central America (Stuart, 1954) and subsequently disappeared from the corridor in Guatemala and Chiapas. Specimens of a *coccifer*-like toad collected by Stuart in the vicinity of Jacaltenango, Departamento Huehuetenango, Guatemala, are much larger than either the Central American or Mexican specimens of *coccifer.* A final commitment on the systematic status must await a thorough study of this group of toads.

Males of this species were calling from a grassy rain-pool in open scrub forest at the edge of Juchitán on July 6, 1956. The call is a low "whirrr." The calling males were sitting in the shallow water at the edge of pond, where they were hidden by the grass. None was observed in open water, as is characteristic of calling males of *Bufo canaliferus* and *marmoreus.*

Bufo marinus Linnaeus

Oaxaca: Agua Caliente; Guichicovi (3); Mixtequilla; Tolosita (6); Tehuantepec (37); Tuxtepec; Unión Hidalgo. *Veracruz:* Ciudad Alemán (4); Cosamaloapan; Cuatotolapam (19); 20 km. SE of Jesús Carranza (4); 38 km. SE of Jesús Carranza (10); 20 km. NE of Jesús Carranza (4); Novillero.

This large toad is abundant throughout the lowlands of the isthmus. The loud rattling call of males was heard on rainy nights throughout the summer. In March, 1956, several adults were found in a small cave back of a spring at Agua Caliente.

Bufo marmoreus Wiegmann

Oaxaca: Cerro San Pedro (2); Chivela (5); Escurano (3); Juchitán; Salina Cruz (101); Santa Lucía (2); 12 km. S of Santiago Chivela (11); Santo Domingo; Tapanatepec; Tehuantepec (100); Tequisistlán. *Veracruz:* Alvarado; Coatzacoalcos.

This toad is abundant on the Pacific lowlands, where it inhabits both open and dense scrub forest. On the Gulf lowlands its distribution seems to be limited to xeric coastal habitats. Aside from the specimens from Alvarado and Coatzacoalcos, it is known in Veracruz only from Boca del Río (Langebartel and Smith, 1959:27).

The similarity in size of *Bufo marmoreus* and *valliceps* and their almost completely allopatric ranges suggest that the two species may be in competition at any one locality. Nevertheless, both were calling from a small rocky stream south of Santiago Chivela on July 6, 1956.

On the night of July 6, 1958, an estimated 400 toads of this species made up a breeding congregation near Salina Cruz. The site was a shallow muddy pond about 20 x 40 meters located in an area cleared of scrub forest; the banks of the pond were devoid of vegetation (Pl. 5, fig. 2). Breeding in the same pond were *Rhinophrynus dorsalis* and *Diaglena reticulata.* The following morning no more than a dozen *Bufo* were found in the pond, but several individuals were found beneath debris and in small burrows near the pond. On July 7, 1958, large numbers of tadpoles and recently metamorphosed young were in a shallow grassy pool just east of Salina Cruz.

Taylor (1943b:347) referred certain specimens from Tehuantepec to *Bufo perplexus,* a species closely related to *Bufo mar-*

moreus. Evidence to be presented elsewhere shows that *perplexus* does not occur in the isthmus.

Bufo valliceps valliceps Wiegmann

Oaxaca: Guichicovi (2); Matías Romero; 32 km. N of Matías Romero (2); Nueva Raza; Río Sarabia (3); Santa María Chimalapa (14); Santiago Chivela; 12 km. S of Santiago Chivela (5); Santo Domingo (5); Tolosita (7). *Veracruz:* Acayucan (3); Alvarado; Amatitlán; Ayentes; Cosamaloapan (3); Cosoleacaque (6); Cuatotolapam (14); Hueyapan; 20 km. ENE of Jesús Carranza (6); 20 km. S of Jesús Carranza; 25 km. SE of Jesús Carranza (23); 35 km. SE of Jesús Carranza; 60 km. SW of Jesús Carranza (5); La Oaxaqueña (4); Novillero (4); San Lorenzo (5).

Individuals were found in both wet and dry seasons. In the dry season they were most frequently found in rainforest, whereas in the rainy season breeding congregations were found in savannas as well. This toad occurs throughout the Gulf lowlands and on the Pacific slopes and in the Grijalva Valley of Chiapas and Guatemala, but not on the Pacific lowlands of the isthmus.

I have not been able to recognize individuals referrable to the race *macrocristatus.* Firschein and Smith (1957:219) described *macrocristatus* from the mountains of eastern Oaxaca and referred to it specimens from the Gulf lowlands of northern Chiapas. None of the present material shows the hypertrophied cranial crests supposedly characteristic of *macroaristatus,* nor do specimens from the isthmus resemble the population in the Grijalva Valley being described by L. C. Stuart, who will discuss the variation in, and the valadity of, the named populations of *valliceps.*

Five specimens from San Lorenzo, Veracruz (USNM 123516-20), were identified as *Bufo cristatus* by Smith (1947:408). Firschein (1950: 83) redefined the *cristatus* group of *Bufo* and assigned these specimens to *valliceps.*

Eleutherodactylus alfredi Boulenger

Oaxaca: Tolosita (2). *Veracruz:* 35 km. SE of Jesús Carranza (6).

These specimens were collected in rainforest. Shreve (1957: 247) pointed out the close resemblance between *E. alfredi* and *E. conspicuus* from Piedras Negras, Guatemala, and treated them as subspecies. Examination of the specimens from the isthmus, together with seven from central Veracruz and one from Teapa, Tabasco, suggests an even closer relationship. *Eleutherodactylus conspicuus* was diagnosed by Taylor and Smith (1945:567) as differing from *alfredi* "in lacking a tarsal fold, in having shorter hind legs with the tibiotarsal articulation reaching only to the nostril instead of beyond the tip of the snout; the vomerine teeth barely reach the posterior level of the choanae." The specimen from

Teapa has the vomerine teeth reaching to the posterior edge of the choanae; in the eight specimens from the isthmus the teeth reach the posterior edge of the choanae in two and to the middle of the choanae in six; in seven specimens from central Veracruz the teeth reach the posterior edge of the choanae in two and to the middle in five. The tibiotarsal articulation extends beyond the tip of the snout in the specimen from Teapa and in two from central Veracruz; in three specimens from the isthmus and in one from central Veracruz it extends only to the nostril; in the others it extends to the snout. The tarsal fold is absent in the specimen from Teapa, in three from the isthmus, and in all those from central Veracruz; it is weakly present in the others.

In the light of this evidence there seems to be little justification in recognizing two species or even two subspecies in this group. Consequently, *Eleutherodactylus conspicuus* Taylor and Smith (1945) is here placed in the synonymy of *Eleutherodactylus alfredi* Boulenger (1898), a species with a range extending from Cuautlapan and Potrero Viejo in central Veracruz southward and eastward in forested habitats to western El Petén, Guatemala.

Eleutherodactylus natator Taylor

Veracruz: 35 km. SE of Jesús Carranza (3); 38 km. S of Jesús Carranza; 55 km. SE of Jesús Carranza.

The snout-vent length is 42.0 mm. in a male and averages 59.5 mm. in three adult females. The tarsal fold is low and extends about half the length of the tarsus; the first and second fingers are subequal in length; the tibiotarsal articulation extends beyond the tip of the snout. The patches of vomerine teeth lie between the posterior margins of the choanae. The throat and belly are immaculate, and the soles of the feet are dark. In the isthmus this species can be distinguished from *Eleutherodactylus rugulosus* by less rugose skin on the dorsum and absence of dark ventral mottling.

The specimens reported here extend the known range of *natator* eastward from Camotlán, Oaxaca; northward in Veracruz the species inhabits foothills as far north as Huatusco.

Eleutherodactylus rhodopis Cope

Oaxaca: 30 km. N of Matías Romero; Río Sarabia (5); Tapanatepec (87); Tolosita (6); between Zanatepec and Tapanatepec. *Veracruz:* 25 km. SE of Jesús Carranza; 35 km. SE of Jesús Carranza (2); 22 km. SSW of Jesús Carranza; 20 km. ENE of Jesús Carranza (7); Minatitlán; Tapalapan (5).

For the purposes of the present study I am not recognizing *Eleutherodactylus beati, E. dorsoconcolor,* and *E. venustus* as specifically, or even subspecifically distinct from the earlier named *E. rhodopis.* Probably these are mere color varieties of a single species.

In the dry season frogs of this species were in humid forests, where they were most frequently found along small streams and in ravines. The species is widespread in the Gulf lowlands, but does not occur on the Plains of Tehuantepec. It does inhabit the Pacific slopes on the foothills of the Sierra Madre de Chiapas, the western part of which extends into eastern Oaxaca near Tapanatepec.

Eleutherodactylus rugulosus Cope

Oaxaca: La Princesa (30); Modelo; Santa Lucía (10); Tapanatepec (26); Tehuantepec (6); Tres Cruces (8). *Veracruz:* Tapalapan (5).

In addition to the specimens from the lowlands of the isthmus, for the purposes of the following discussion, I have included data on two specimens from the southern slopes of the Sierra del Sur in Oaxaca (Mirador and Chacalapa) and on several specimens from Los Tuxtlas in Veracruz (Los Chaneques, 67; Salto de Eyipantla, 35; and San Andrés Tuxtla, 11).

Frogs of the *Eleutherodactylus rugulosus* complex occur from southern Veracruz and Sinaloa southward through Central America. Taylor (1940:401) described *E. vocalis* from Hacienda El Sabino, Michoacán; Taylor and Smith (1945:580) described *E. avocalis* from Tres Cruces, Oaxaca. These have been considered as species distinct from *rugulosus,* which is known to occur in Veracruz, Guerrero, and Chiapas southward into Central America. Although the large number of specimens collected in the isthmus does not aid in defining the ranges of the taxa involved, these specimens do give some idea of the variation in certain characters in a given population.

In specimens from Los Tuxtlas the tarsal fold is well-developed and extends two-thirds to three-fourths the length of the tarsus; the tibiotarsal articulation reaches the nostril and sometimes slightly beyond the tip of the snout. In males the tympanum is nearly equal to the diameter of the eye; in females it is about one-half the diameter of the eye. The posterior surfaces of the thighs are dark brown or black with whitish or cream-colored spots, flecks, or irregular mottling. The tarsal fold is dark; the throat is pale in some individuals, but in most is mottled with dark brown or gray flecks. Individuals from La Princesa near the continental divide in Oaxaca show the same variation in body proportions and development of the tarsal fold. The posterior surfaces of the thighs are dark brown in-distinctly mottled with lighter brown. The throat is dark brown. Specimens from the Pacific slopes of Oaxaca, including the Plains of Tehuantepec, have dark brown thighs mottled with dusty cream. The tibiotarsal articulation extends slightly beyond the tip of the snout in all specimens. In males the tympanum is equal to about two-thirds the diameter of the eye. Duellman (1958b:6) discussed the variation in these characters in populations in Colima, Jalisco, and Michoacán.

Until the extent of variation of these characters is known throughout the range of *rugulosus*, the recognition of populations either as species or subspecies seems superfluous. Consequently, I have used the oldest name; this does not necessarily imply, however, that all populations of *rugulosus (sensu lato)* are conspecific.

Of the 200 specimens examined, 15 have a middorsal stripe that is red or yellow. The iris varies from a copper to a dark golden color and shines bright red at night. Many of the specimens are juveniles; these were collected in the dry season, at which time they were found beneath rocks along streams, in road culverts where there was some water, and in holes in banks and cliffs.

Microbatrachylus pygmaeus Taylor

Oaxaca: La Princesa (5); Matías Romero (9); Río Sarabia (41); Tolosita (2). *Veracruz:* Jesús Carranza; 20 km. ENE of Jesús Carranza.

The specimens listed above vary widely in color patterns; some of the patterns are characteristic of certain named "species": *albolabris, imitator, lineatissimus,* and *minimus.* The large series from the Río Sarabia contains all of the color patterns; this series was obtained in one small ravine in the rainforest. At least in the isthmian region, this species does not inhabit the Pacific slopes and lowlands.

Syrrhophus leprus Cope

Oaxaca: 33 km. N of Matías Romero; Santa Efigenia. *Veracruz:* San Lorenzo.

Although the type locality is stated to be Santa Efigenia on the Pacific slopes of the Sierra Madre de Chiapas in eastern Oaxaca, the type specimen probably came from the northern slopes of the mountains. All other known specimens are from the Gulf slopes and lowlands, and from several localities in Los Tuxtlas. Details concerning specimens from the isthmus and other parts of the range were given by Duellman (1958c:8).

Smith (1947:408) reported a specimen of *Syrrhophus verruculatus* Peters from San Lorenzo, Veracruz; he stated that this specimen (USNM 123530) could not be S. *leprus,* because it had a gray belly, nor S. *cystignathoides,* because of the dark and light dorsal coloration. Firschein (1954:57) in his review of the species of *Syrrhophus* in eastern México referred the specimen to S. *cystignathoides.* The specimen is in poor condition. Nevertheless, specific determination is possible. Numerous specimens of S. *leprus* from Los Tuxtlas have gray bellies; some have heavier pigmentation than the specimen from San Lorenzo. In preservative the dorsum is dark brown with lighter mottling. There is little doubt that the specimen from San Lorenzo is a *Syrrhophus leprus,* an abundant and widespread species in the humid Gulf lowlands of southern México, and not *verruculatus,* if this is a valid species (see Firschein, *op. cit.*:58), and not *cystignathoides,* a species known from San Luis Potosí southward to central Veracruz.

Syrrhophus pipilans pipilans Taylor

Oaxaca: Cerro Arenal; Cerro San Pedro; 6 km. N of Chivela; 14 km. W of Tehuantepec (2).

In the isthmian region this frog is known only from the Pacific slopes and the Plains of Tehuantepec. Males call from the ground and from trees to heights of about four meters. The call is a single, high, long "peep."

Engystomops pustulosus Cope

Oaxaca: Chivela; La Ventosa (3); Santo Domingo; Tapanatepec (14); Tehuantepec (61); Unión Hidalgo (62). *Veracruz:* Acayucan; Cuatotolapam (7); 10 km. SE of Hueyapan (11).

Large congregations were breeding at Tehuantepec on July 5, at Tapanatepec on July 13, and at Hueyapan on July 24, 1956. The frogs were breeding in open ponds in scrub forest and savanna; none was found in the rainforest. Males call while floating on the water (Pl. 7, fig. 1); the call is a soft "do-ing, do-ing" with a rising tone on the last note. Numerous individual egg masses were along the bank of a pond near Tehuantepec; one large composite egg mass there had a surface area of about one square meter (Pl. 7, fig. 2). The large series from Unión Hidalgo was obtained by digging specimens out of a dry sandy river bank in the dry season. Some of the individuals were buried to a depth of 25 centimeters.

In life individuals from the Pacific lowlands were dull brown and gray; those from Acayucan were dark chocolate brown to black with pink or red blotches, forearms, and dorsal stripe. Not all specimens from the Atlantic lowlands are so colored; individuals from Cordoba and Mirador, Veracruz, are like those from Tehuantepec.

Leptodactylus labialis Cope

Oaxaca: Agua Caliente; Chivela (2); Matías Romero (12); 33 km. N of Matías Romero (4); Mixtequilla; Santa Efigenia; Tapanatepec; Tehuantepec (38); Tolosita (2); 33 km. W of Zanatepec (49). *Veracruz:* Acayucan (3); Ciudad Alemán; Cuatotolapam (10); Hueyapan; La Oaxaqueña (4); 38 km. SE of Jesús Carranza; 20 km. ENE of Jesús Carranza; Novillero (3); San Lorenzo (2).

Although *Leptodactylus labialis* does not appear to be so abundant as *Leptodactylus melanonotus,* the former was found throughout the lowlands of the isthmus. In the dry season individuals were found along streams, and in the rainy season breeding congregations were found in rain pools, marshes, ponds, and even small puddles. The call is a slow "wort, wort, wort." Males call beneath the water and from beneath rocks and from holes in the ground. The average snout-vent length of eight adult males is 37.2 mm. A completely metamorphosed juvenile obtained at Hueyapan on July 24, 1956, has a snout-vent length of 11 mm.

Leptodactylus melanonotus Hallowell

Oaxaca: Agua Caliente (25); Cerro Arenal (2); Cerro Quiengola (3); Cerro San Pedro (3); Chivela (2); Coyol; Juchitán; Matías Romero (11); Mixtequilla (2); Papaloapan (2); Salazar (9); Salina Cruz; 11 km. S of Santiago Chivela; Tapanatepec (17); Tehuantepec (176); Tolosita; Unión Hidalgo; 27 km. W of Zanatepec (6). *Veracruz:* Acayucan; Cuatotolapam (9); Cosoleacaque; 20 km. ENE of Jesús Carranza (2); 20 km. SE of Minatitlán (2); Novillero; San Lorenzo (6).

This frog is abundant throughout the lowlands of the isthmus, where in the dry season individuals were found along streams and beneath rocks at a spring seepage. In the rainy season males were calling from nearly every bit of standing water. The call is a soft clicking sound resembling that made by striking two small stones together. The average snout-vent length of ten adult males is 41.8 mm. There is considerable variation in the extent of the yellowish brown glandular areas on the belly. Some have none, whereas others have a broad area on the chest, a band along the flanks, and a thin band across the lower abdomen. Individuals collected in the dry season vary in the same fashion as do those collected in the rainy season, at which time they were breeding. The glands are equally well-developed in adults of both sexes, and were present in some juveniles with snout-vent lengths of less than 20 mm. Apparently the development of the glands is not associated with maturity, sex, or size.

Diaglena reticulata Taylor

Oaxaca: Cerro Arenal; Chivela; Salina Cruz (26); San Antonio (3); Tehuantepec (2); 8.6 km. W of Tehuantepec (11); Zarzamora.

Breeding congregations of this rare frog were found 8.6 kilometers west of Tehuantepec on July 5, 1956, and at Salina Cruz on July 6, 1958. Both choruses took place immediately after torrential rains. In both instances the frogs were in and about open muddy pools in the scrub forest (Pl. 5, fig. 2); males called from the bank near the water, and clasping pairs were found only on land (Pl. 8, figs. 1-2). The call is a loud, nasal "braaa," two to three seconds in duration. Amplexus is axillary.

The dorsal ground color is light yellowish green tending towards olive on the head and fading to yellow on the flanks. The ventral surfaces, including the vocal sac, are white; the iris is golden and flecked with black. The present series agrees well with the description of *reticulata* (based on two specimens) given by Taylor (1942:60). A detailed analysis of variation, comparison with related species, and descriptions of tadpoles are reserved for a future report.

Hyla baudini Duméril and Bibron

Oaxaca: Bisilana; Cerro Quiengola (2); Cerro San Pedro; Coyol; Matías Romero (12); Mixtequilla; Río Sarabia (7); Salazar; San Antonio; 11 km. S of Santiago Chivela; Santo Domingo (3); Tapanatepec (2); Tehuantepec (23); Tolosita. *Veracruz:* Acayucan; Amatitlán; Ciudad Alemán (3); Cosamaloapan (2); Cuatotolapam (15); 10 km. SE of Hueyapan; 20 km. S of Jesús Carranza; 38 km. S of Jesús Carranza (2); 20 km. ENE of Jesús Carranza (4); La Oaxaqueña (2); Minatitlán (2); Naranja (3); Novillero (9); Río de las Playas (2); San Lorenzo (5); Tapalapan (2).

Commonly found on both sides of the isthmus, this large tree frog nearly always is associated with trees; it is not found in the savannas, although it breeds in savannas adjacent to rainforest. It appears to be somewhat more abundant in scrub forest than in rainforest. In the daytime individuals were found under the outer sheaths of banana plants, in the axills of leaves of elephant ears (*Xanthosoma*), in cavities in trees, and on shaded limbs in the forest. Recently metamorphosed individuals having snout-vent lengths slightly more than 20 mm. were found in the latter part of July.

Hyla ebraccata Cope

Oaxaca: Donají (17); 43 km. N of Matías Romero (27); Sarabia (6); Tolosita (3); Ubero (17). *Veracruz:* Aquilera.

This small species was found only in forested areas, where calling males were on bushes and trees around rain pools. The call is a harsh squawk repeated at intervals of 15 to 20 seconds, followed by a minute or more of silence, and then repeated. Clasping pairs were found on bushes and in the water.

The dorsum bears a dark chocolate brown hour glass-shaped mark, which in some individuals is broken into a large mark posteriorly and a smaller triangular one on the head and nape. The dorsal ground color varies from pale cream or ivory to yellow or tan. The intensity of the dorsal pigmentation is subject to rather rapid change. The flanks, hands, and anterior part of the venter are lemon yellow; the feet, thighs, and posterior part of the venter are golden yellow. The dorsal surface of the shank is yellow to tan with chocolate brown bars or spots; the heel is pale yellow. There is a dark brown bar in the loreal region and a dark brown bar extending posteriorly from the eye to a point above the insertion of the forelimb. The iris is a copper color. The toes are completely webbed; the fingers, one-third webbed. There is a small axillary web that is evident when the forelimbs are at right angles to the body. Twenty males have an average snout-vent length of 28.1 mm.; three females, 35.3 mm. There are no nuptial tuberosities on the pollex of breeding males.

This species has been collected at Coyame and Catemaco in Los Tuxtlas and at various localities in Tabasco; it apparently ranges eastward from southern Veracruz, México, in humid forests to El Petén, Guatemala.

Hyla loquax Gaige and Stuart

Oaxaca: Donají (7); 43 km. N of Matías Romero (21). *Veracruz:* 19 km. N of Acayucan (4); Aquilera (3); 8 km. SW of Coatzacoalcos (36); Cuototolapam (11); Naranja (13); San Lorenzo (3).

In the isthmus this species is known only from the humid forests of the Gulf lowlands; it is also known from Boca del Río, Veracruz, and from Teapa and Villa Hermosa, Tabasco.

Calling males were found on aquatic plants above the water in deep ponds in the forest where it was necessary for the collector to wade waist-deep in water to obtain them. The call is a loud "hah-onk." Individuals, when active at night, are yellowish tan above with light olive green spots. The flanks, belly, and vocal sac are yellow, and the anterior and posterior surfaces of the thighs and webbing of the feet are bright orange-red or tomato red. Individuals found during the day are grayish brown with olive markings or reddish brown with black markings. Sleeping individuals are ivory-gray with faint gray markings. The iris is a bright copper color. Fifteen adult males have an average snout-vent length of

41.7 mm.; they have no horny nuptial pads on the pollex.

The relationships of this species are with *Hyla rickardsi* Taylor, a species known only from the foothills of the Sierra Madre Oriental in the states of Puebla and Veracruz. The distinguishing characteristics of these species are given in Table 1. Living individuals may be distinguished immediately by the flash colors on the thighs—red in *loquax* and yellow in *rickardsi.* The calls of the two species are distinctly different; that of *rickardsi* is a high-pitched, loud rattle continued for several seconds, notably different from the goose-like honk of *loquax.*

TABLE 1.—COMPARISON OF CERTAIN CHARACTERS IN HYLA LOQUAX AND HYLA RICKARDSI

CHARACTER	*loquax*	*rickardsi*
Toe webbing	Full	Three-fourths
Finger webbing	Three-fourths	One-half
Average snout-vent length (♂)	41.7 mm.	37.4 mm.
Tympanum/eye (♂)	63.2%	55.8%
Dorsal leg pattern	Barred	Unmarked
Tarsal fold	Tubercular	Absent
Tarsal stripe	Absent or indistinct	Broad, indistinct, or absent
Dorsolateral stripe	Absent	Present
Light line over anus	Broad	Narrow
Flash colors	Red	Yellow
Iris color	Copper	Bronze

The three specimens from San Lorenzo, Veracruz (USNM 123513-5), were identified as *Hyla rickardsi* by Smith (1947:409). The flash colors have faded in preservative, and so are of no aid in identifying these specimens. Two are adult females with snout-vent lengths of 35 and 39 mm. In possessing a relatively large tympanum and barred thighs, and in lacking a dorsolateral stripe they are typical of *loquax,* but in the amount of webbing on the hands and feet, broad tarsal stripe, and narrow anal stripe they are like *rickardsi.* The third specimen, a juvenile, has a snout-vent length of 25 mm. In coloration it resembles the adults; it has more distinct bars on the limbs. On the basis of geography these specimens should be *loquax,* for the closest known record of *rickardsi* is more than 200 kilometers to the northwest, whereas *loquax* is known from several localities around San Lorenzo.

Shannon and Werler (1955:383) described *Hyla axillamembrana* from the lower southern slopes of Los Tuxtlas. The unique type is a small male (27 mm. snout-vent). I have examined the type and find no great differences between it and small specimens of *loquax.* It is not possible to determine the color of the thighs, nor was this information given in the description. *Hyla axillamembrana* is here considered to be a synonym of *Hyla loquax.*

Hyla microcephala martini Smith

Oaxaca: Donají (15); 43 km. N of Matías Romero (19); Río Sarabia (2); Sarabia (11); Tolosita. *Veracruz:* Acayucan (17); Alvarado (41); Aquilera (21); 8 km. SW of Coatzacoalcos (10); Cosoleacaque (26); 10 km. SE of Hueyapan; Naranja (3); Novillero.

This frog is abundant in the Gulf lowlands of the isthmus, where large breeding congregations were found in grassy ponds on the savannas and in openings in the forest. Most frequently males were calling from grasses and reeds in the ponds; many individuals were perched precariously on thin blades as high as one meter above the water. The call is a series of low squeaks.

Individuals found at night were pale yellow above with light brown lines arranged in an irregular pattern on the back, but often forming a cross or an X-shaped mark in the scapular region. There is a brown stripe from the nostril to the eye and thence to the groin. Anteriorly this stripe is bordered above by a thin white or cream-colored line. Numerous small brown flecks are scattered on the back and dorsal surface of the shank. In most specimens there are thin transverse brown bars on the shank. The thighs and undersides of the limbs are golden yellow; the belly and vocal sac are lemon yellow. The iris is yellowish brown. During the day individuals assume a pale reddish tan ground color with darker brown markings. Twenty-five adult males from Alvarado have an average snout-vent length of 24.1 mm.

Hyla picta Günther

Oaxaca: Donají (8); Sarabia (11); Tolosita (15); Ubero (6). *Veracruz:* 19 km. N of Acayucan (4); Alvarado (5); Aquilera; 8 km. SW of Coatzacoalcos; 10 km. SE of Hueyapan (7); Lerdo de Tejada; Tula (3).

Widespread in the forests, scrub, and savannas on the Gulf lowlands of the isthmus, these frogs were found breeding at numerous localities. Males call from grasses and bushes growing in and about ponds. The call is a high-pitched insect-like trill. At night these frogs are pale yellow above; they change to light grayish tan during the day. A dark stripe extends from the nostril to the eye and thence posteriorly to a point between the axilla and groin. Above this dark stripe is a broader white stripe. Scattered on the dorsum are brown flecks or spots; the shanks are marked with poorly-defined cross-bars. The thighs are deep yellow below and paler above with scattered dark flecks. The belly is white, and the vocal sac is yellow. The iris is golden. Twenty males have an average snout-vent length of 21.5 mm.; three females, 24.0 mm.

Hyla robertmertensi Taylor

Oaxaca: Tapanatepec (28); 7.5 km. NW of Tapanatepec (38); 7.2 km. WNW of Zanatepec (77).

This species was found in the isthmian region only on the Pacific lowlands at the southern base of the western part of the Sierra Madre de Chiapas. On July 13, 1956, many large choruses were discovered. The calling males were on reeds and thorn scrub in and at the edge of temporary ponds; the call is a cricket-like "creak-creack," quickly followed by a series of notes "creak-eek-eek-eek-eek."

At night the dorsal ground color is pale yellow; this changes to pinkish buff during the day. There is a grayish or brown dark stripe from the nostril to the eye; the stripe continues to the groin. This dark stripe is bordered above by a narrow white stripe. The belly is white, and the vocal sac is yellow. The iris is dull reddish brown. Twenty-five males have an average snout-vent length of 24.7 mm.

Hyla staufferi Cope

Oaxaca: Chivela; Huilotepec (5); Juchitán (4); Matías Romero (4); 25 km. N of Matías Romero; Mixtequilla (4); Río Sarabia (11); 11 km. S of Santiago Chivela; Sarabia (3); Tapanatepec (67); Tehuantepec (66); Tolosita (2); Ubero; Unión Hidalgo; Zanatepec (6). *Veracruz:* Acayucan (7); Alvarado (3); Amatitlán; Aquilera; Ciudad Alemán (3); 8 km. SW of Coatzacoalcos (9); Cosamaloapan (4); Cosoleacaque (8); 10 km. SE of Hueyapan; Lerdo de Tejada; Novillero (6); Tula (2).

This is the only species of small hylid that crosses the isthmus. Calling males were found in and about ponds on the savannas in southern Veracruz, in ponds in open forest in northern Oaxaca (not in forest pools), and in temporary pools in the scrub forest on the Pacific lowlands. Individuals usually called from bushes and reeds in or at the edge of ponds. The call is a short "braaa." Dates of breeding choruses indicate that by the time the other small species of hylids in the Gulf lowlands reach the peak of their breeding season, that of *H. staufferi* is essentially over; no large breeding congregations were found in July. On July 8, 1956, two metamorphosing young were found clinging to blades of grass in a pond; they had snout-vent lengths of 8 and 9 mm. and tail stumps less than 3 mm. in length. Others were found on July 13 and 26. The juveniles are nearly unicolor olive green above and white below.

In life the adults vary greatly in color pattern. The dorsal ground color is yellowish tan to olive brown with olive brown or dark brown spots, some of which in certain individuals are connected to form longitudinal dark stripes. On the posterior surface of the thighs are small white flecks. The belly is white, and the vocal sac is a rich yellow. Twenty males have an average snout-vent length of 26.3 mm.; they have no horny nuptial pads. No noticeable differences in either color or body proportions were found between the populations on either side of the isthmus.

Hylella sumichrasti Brocchi

Oaxaca: Cerro Arenal (5); Cerro San Pedro (2); Escurano; La Concepción (41); Portillo Los Nanches (6); San Antonio (16); 11 km. S of Santiago Chivela (18); Santa Lucía (7); Tapanatepec (5); Tehuantepec (8); Tenango (49); Tres Cruces (19).

With the exception of the series from 11 kilometers south of Santiago Chivela, most of these specimens were found in small arboreal bromeliads during the dry season. Males were found along a clear, shallow, rocky stream south of Santiago Chivela on July 6, 1956. The frogs were calling from bushes and rocks in and along the stream. When disturbed, they jumped into the water and floated downstream until they were able to hold onto a rock or other object. The call is a loud "bra-a-ah." In breeding individuals the dorsum is pale yellow; the belly is white, and the vocal sac is yellow. The iris is pale golden yellow. Eighteen males have an average snout-vent length of 25.2 mm. All have dark brown nuptial tuberosities on the pollex.

Certain diagnostic characters of this species as given by Taylor (1943a:50) and Taylor and Smith (1945:598) are in need of revision. *Hylella sumichrasti* has been characterized as having no vocal sac, rarely having vomerine teeth, and as having a relatively smooth throat. The vocal sac in breeding males is quite evident; it is single, median, and when expanded, spherical. The openings into the vocal sac are narrow slits along the inner posterior border of the jaw rami. Of 151 specimens studied, 74 have vomerine ridges between the choanae, and 36 of these have one to three teeth on each ridge. The belly and undersurfaces of the thighs are granular; the throat is only somewhat less so. The granular condition may be correlated with breeding, for specimens obtained from bromeliads in the dry season had rather smooth throats. It seems that the vocal sac atrophys in the non-breeding season. These seasonal changes may account for the diagnoses given by Taylor (*op. cit.*) and Taylor and Smith (*op. cit.*); likewise, since many of the specimens obtained by Smith in the dry season were juveniles and subadults, the development of the vomerine ridges could not be diagnosed properly.

The range of this species encompasses the Pacific slopes of the Isthmus of Tehuantepec eastward to the upper Cintalapa Valley and vicinity of Tonalá in western Chiapas. Priscilla Starrett collected tadpoles of *H. sumichrasti* from a stream 19 km. N of Arriaga, Chiapas. These limited observations on the ecology of this frog suggest that it breeds in the fast-moving streams of the Pacific slopes, and that it seeks shelter in arboreal bromeliads during the dry season.

Phrynohyas modesta Taylor and Smith

Oaxaca: Tuxtepec. *Veracruz:* 20 km. S of Jesús Carranza; 20 km. ENE of Jesús Carranza (2); Minatitlán.

I have not collected this species in the isthmus. The locality records indicate that the range is discontinuous (Duellman, 1956: 27). The species occurs on the humid Pacific slopes from south-central Chiapas eastward to El Salvador and on the humid Gulf lowlands from southern Veracruz eastward into Tabasco, but is unknown from the dry Pacific slopes and plains in the isthmus.

The acquisition of several specimens of this species in southern Veracruz, Tabasco, and Oaxaca, together with a knowledge of the variation displayed by *Phrynohyas spilomma,* suggests that *modesta* may be a color variety of *spilomma.*

Phrynohyas spilomma Cope

Oaxaca: Tapanatepec (3). *Veracruz:* Amatitlán (12); Chacaltianguis (2); Ciudad Alemán (6); Cosamaloapan; Novillero (3).

Like the preceding species, this frog is unknown from the arid Pacific lowlands of the isthmus; its presence at Tapanatepec, a locality situated in more mesic conditions than prevail on the Plains of Tehuantepec, indicates that it may have a distribution on the Pacific slopes much like that of *P. modesta.* Furthermore, this frog was not detected in the rainforests of the Gulf lowlands; in that region it was found only in scrub forest and savanna.

On July 26, 1956, numerous choruses of these frogs were heard between Ciudad Alemán and Tlacotalpan, Veracruz. The call is a loud, nasal "grawl" repeated continuously. The males call from the water. Several clasping pairs were found in shallow grassy ponds amidst the scrub forest. The ground color varies from reddish brown to tan with dark brown dorsal markings. The iris is golden, and the vocal sacs are dark olive brown. After a light shower during the dry season, six individuals were found on the low branches of trees at night near Ciudad Alemán.

Phyllomedusa callidryas taylori Funkhouser

Oaxaca: Donají (9); Sarabia (8); Tolosita (6); Ubero (27). *Veracruz:* Alvarado (7); Aquilera; Berta; Coatzacoalcos (9); 10 km. SE of Hueyapan (5); Naranja (17).

In life this frog presents a striking array of colors. The dorsum varies from pale green to dark olive green; there may be scattered whitish or cream-colored spots on the back. On the flanks are bright yellow to deep cream-colored vertical bars separated by pale blue or purple interspaces. The thighs and undersurfaces of the hind limbs are golden orange; the belly is yellow, and the throat is cream-colored. The iris is crimson; the transparent part of the lower eyelid has golden reticulations. When the frog is resting, the forefeet are folded beneath the throat, and the limbs are folded tightly against the body. In this position and with the eyes closed and head flattened, this gaudy frog assumes the appearance of a small elliptical green leaf.

Throughout the month of July, 1956, *Phyllomedusa* was breeding in ponds in or adjacent to the rainforest in northern Oaxaca and in southern Veracruz. Only at Alvarado was it found breeding in a grassy pond. Males and females alike were found on bushes and trees in and around the ponds. The call is a single "wank." Amplexing males continue to call, but the call is softer and less nasal in quality. The eggs are encased in pale green gelatin and attached to leaves on branches overhanging the water. Three egg clutches contained 38, 41, and 46 eggs.

Phyllomedusa dacnicolor Cope

Oaxaca: Escurano; Tehuantepec.

Although it is abundant on the Pacific lowlands to the northwest in Guerrero, Michoacán, and Colima, this species is known only from two specimens from Tehuantepec. There is no apparent physical barrier to their distribution in the isthmus; in the Balsas Basin the species lives in a hotter, more arid environment than that at Tehuantepec.

Gastrophryne usta Cope

Oaxaca: Santa Efigenia; Tehuantepec (10); 24 km. W of Tehuantepec; Tolosita (2). *Veracruz:* Ayentes (6); La Oaxaqueña; Novillero (2); San Lorenzo.

Calling males were found in open scrub forest near Tehuantepec and in savannas near Novillero. The specimens from Tolosita were found under cover in a clearing in the forest (Fugler and Webb, 1957:106).

Specimens from the Pacific lowlands are typical of *Gastrophryne usta gadowi* Boulenger in possessing a thin line on the posterior surface of the thighs and a thin line from the snout to the vent. Of nine specimens from the Gulf lowlands (Ayentes, Novillero, and San Lorenzo), seven have a middorsal line; this is narrow in four and wide in three. Five have the stripes on the thighs. Two specimens from the middle of the isthmus (Tolosita) have no stripes on the thighs; one has a thin middorsal line, and the other has a broad line. The adult males have a black throat; females have a mottled one. The brown reticulations on the bellies of specimens from the Gulf lowlands is bolder than on specimens from the Pacific lowlands. The presence of certain characters supposedly diagnostic of the subspecies *gadowi* (line on dorsum and thighs) in the population of *usta* in southern Veracruz suggests that a redefinition of the ranges of these subspecies will be in order when sufficient material is available to delimit them accurately. For the present I prefer to consider all specimens from the isthmus solely as *Gastrophryne usta* without refering them to subspecies.

Rana palmipes Spix

Oaxaca: Matías Romero (11); 11 km. S of Santiago Chivela; Santo Domingo; Sarabia. *Veracruz:* Coatzacoalcos; Cuatotolapam; 25 km. SE of Jesús Carranza (4); Tlacotalpan (2); Tula.

Adults were found along streams and in marshes in savannas and rainforest. These frogs are wary and difficult to capture, even at night. *Rana palmipes* is another species that has a discontinuous distribution in the isthmus. The species does not occur on the Pacific lowlands of the isthmus, but does occur on the more humid Pacific slopes of Chiapas and Guatemala.

Tadpoles were found in a small sluggish tributary to the Río Sarabia.

Rana pipiens Schreber

Oaxaca: Agua Caliente; Cerro Quiengola; Escurano (14); Río Sarabia (2); Tapanatepec (5); Tehuantepec (24). *Veracruz:* Acayucan; Cuatotolapam (15); Jesús Carranza (2); 20 km. S of Jesús Carranza (11); 25 km. SE of Jesús Carranza; 20 km. ENE of Jesús Carranza (10); San Lorenzo (10).

As in most other places in México and northern Central America, this species occurs wherever there is permanent water. Males were heard calling from woodland ponds and from savanna ponds.

SUMMARY

Investigations of the amphibians and their environments in the Isthmus of Tehuantepec have been presented with the aim of gaining an understanding of the present biological and of the historical events responsible for the present patterns of distribution of amphibians in this region.

The Isthmus of Tehuantepec embraces three major environments—savanna, semi-arid scrub forest, and quasi-rainforest. The rainforest presents an environment noticeably different from the other two and has a different amphibian fauna.

Analysis of present patterns of distribution shows that certain species are restricted to the rainforests on the Gulf lowlands; others live only in the semi-arid scrub forests on the Pacific lowlands. A third group of species lives on both the Gulf and Pacific lowlands; most of these species occur only in the scrub forests or savannas on the Gulf lowlands, but some also inhabit the rainforest. In one way or another the isthmus presents a barrier to the distribution of 75 per cent of the species of amphibians living in the lowlands; it is a greater barrier still to the species inhabiting the highlands on either side.

Present patterns of distribution are attributed to bioclimatic fluctuation in the Pleistocene. In the course of these climatic shifts, tropical environments and their amphibian inhabitants seem to have survided in the isthmian region.

The amphibian fauna of the lowlands of the Isthmus of Tehuantepec consists of 16 genera and 36 species. Systematic studies of all available specimens from the region show that *Eleutherodactylus conspicuus* Taylor and Smith is a synonym of *Eleutherodactylus alfredi* Boulenger and that *Hyla axillamembrana* Shannon and Werler is a synonym of *Hyla loquax* Gaige and Stuart.

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(Continued from inside of front cover)

Vol. 8. 1. Life history and ecology of the five-lined skink, Eumeces fasciatus. By Henry S. Fitch. Pp. 1-156, 26 figures in text. September 1, 1954.

2. Myology and serology of the Avian Family Fringillidae, a taxonomic study. By William B. Stallcup. Pp. 157-211, 23 figures in text, 4 tables. November 15, 1954.

3. An ecological study of the collared lizard (Crotaphytus collaris). By Henry S. Fitch. Pp. 213-274, 10 figures in text. February 10, 1956.

4. A field study of the Kansas ant-eating frog, Gastrophryne olivacea. By Henry S. Fitch. Pp. 275-306, 9 figures in text. February 10, 1956.

5. Check-list of the birds of Kansas. By Harrison B. Tordoff. Pp. 307-359, 1 figure in text. March 10, 1956.

6. A population study of the prairie vole (Microtus ochrogaster) in northeastern Kansas. By Edwin P. Martin. Pp. 361-416, 19 figures in text. April 2, 1956.

7. Temperature responses in free-living amphibians and reptiles of northeastern Kansas. By Henry S. Fitch. Pp. 417-476, 10 figures in text, 6 tables. June 1, 1956.

8. Food of the crow, Corvus brachyrhynchos Brehm, in south-central Kansas. By Dwight Platt. Pp. 477-498, 4 tables. June 8, 1956.

9. Ecological observations on the woodrat, Neotoma floridana. By Henry S. Fitch and Dennis G. Rainey. Pp. 499-533, 3 figures in text. June 12, 1956.

10. Eastern woodrat, Neotoma floridana: Life history and ecology. By Dennis G. Rainey. Pp. 535-646, 12 plates, 13 figures in text. August 15, 1956.

Index. Pp. 647-675.

Vol. 9. 1. Speciation of the wandering shrew. By James S. Findley. Pp. 1-68, 18 figures in text. December 10, 1955.

2. Additional records and extensions of ranges of mammals from Utah. By Stephen D. Durrant, M. Raymond Lee, and Richard M. Hansen. Pp. 69-80. December 10, 1955.

3. A new long-eared myotis (Myotis evotis) from northeastern Mexico. By Rollin H. Baker and Howard J. Stains. Pp. 81-84. December 10, 1955.

4. Subspeciation in the meadow mouse, Microtus pennsylvanicus, in Wyoming. By Sydney Anderson. Pp. 85-104, 2 figures in text. May 10, 1956.

5. The condylarth genus Ellipsodon. By Robert W. Wilson. Pp. 105-116, 6 figures in text. May 19, 1956.

6. Additional remains of the multituberculate genus Eucosmodon. By Robert W. Wilson. Pp. 117-123, 10 figures in text. May 19, 1956.

7. Mammals of Coahuila, Mexico. By Rollin H. Baker. Pp. 125-335, 75 figures in text. June 15, 1956.

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9. Extensions of known ranges of Mexican bats. By Sydney Anderson. Pp. 347-351. August 15, 1956.

10. A new bat (Genus Leptonycteris) from Coahuila. By Howard J. Stains. Pp. 353-356. January 21, 1957.

11. A new species of pocket gopher (Genus Pappogeomys) from Jalisco, Mexico. By Robert J. Russell. Pp. 357-361. January 21, 1957.

12. Geographic variation in the pocket gopher, Thomomys bottae, in Colorado. By Phillip M. Youngman. Pp. 363-387, 7 figures in text. February 21, 1958.

13. New bog lemming (genus Synaptomys) from Nebraska. By J. Knox Jones, Jr. Pp. 385-388. May 12, 1958.

14. Pleistocene bats from San Josecito Cave, Nuevo León, México. By J. Knox Jones, Jr. Pp. 389-396. December 19, 1958.

15. New Subspecies of the rodent Baiomys from Central America. By Robert L. Packard. Pp. 397-404. December 19, 1958.

16. Mammals of the Grand Mesa, Colorado. By Sydney Anderson. Pp. 405-414, 1 figure in text. May 20, 1959.

17. Distribution, variation, and relationships of the montane vole, Microtus montanus. By Emil K. Urban. Pp. 415-511. 12 figures in text, 2 tables. August 1, 1959.

18. Conspecificity of two pocket mice, Perognathus goldmani and P. artus. By E. Raymond Hall and Marilyn Bailey Ogilvie. Pp. 513-518, 1 map. January 14, 1960.

19. Records of harvest mice, Reithrodontomys, from Central America, with description of a new subspecies from Nicaragua. By Sydney Anderson and J. Knox Jones, Jr. Pp. 519-529. January 14, 1960.

(Continued on outside of back cover)

(Continued from inside of back cover)

20. Small carnivores from San Josecito Cave (Pleistocene), Nuevo León, México. By E. Raymond Hall. Pp. 531-538, 1 figure in text. January 14, 1960.
21. Pleistocene pocket gophers from San Josecito Cave, Nuevo León, México. By Robert J. Russell. Pp. 539-548, 1 figure in text. January 14, 1960.
22. Review of the insectivores of Korea. By J. Knox Jones, Jr., and David H. Johnson. Pp. 549-578. February 23, 1960.
23. Speciation and evolution of the pygmy mice, genus Baiomys. By Robert L. Packard. Pp. 579-670, 4 plates, 12 figures in text. June 16, 1960.

Index Pp. 671-690.

Vol. 10. 1. Studies of birds killed in nocturnal migration. By Harrison B. Tordoff and Robert M. Mengel. Pp. 1-44, 6 figures in text, 2 tables. September 12, 1956.

2. Comparative breeding behavior of Ammospiza caudacuta and A. maritima. By Glen E. Woolfenden. Pp. 45-75, 6 plates, 1 figure. December 20, 1956.
3. The forest habitat of the University of Kansas Natural History Reservation. By Henry S. Fitch and Ronald R. McGregor. Pp. 77-127, 2 plates, 7 figures in text, 4 tables. December 31, 1956.
4. Aspects of reproduction and development in the prairie vole (Microtus ochrogaster). By Henry S. Fitch. Pp. 129-161, 8 figures in text, 4 tables. December 19, 1957.
5. Birds found on the Arctic slope of northern Alaska. By James W. Bee. Pp. 163-211, pls. 9-10, 1 figure in text. March 12, 1958.
6. The wood rats of Colorado: distribution and ecology. By Robert B. Finley, Jr. Pp. 213-552, 34 plates, 8 figures in text, 35 tables. November 7, 1958.
7. Home ranges and movements of the eastern cottontail in Kansas. By Donald W. Janes. Pp. 553-572, 4 plates, 3 figures in text. May 4, 1959.
8. Natural history of the salamander, Aneides hardyi. By Richard F. Johnston and Schad Gerbard. Pp. 573-585. October 8, 1959.
9. A new subspecies of lizard, Cnemidophorus sacki, from Michoacán, México. By William E. Duellman. Pp. 587-598, 2 figures in text. May 2, 1960.
10. A taxonomic study of the Middle American Snake, Pituophis deppei. By William E. Duellman. Pp. 599-612, 1 plate, 1 figure in text. May 2, 1960.

Index Pp. 611-626.

Vol. 11. 1. The systematic status of the colubrid snake, Leptodeira discolor Günther. By William E. Duellman. Pp. 1-9, 4 figs. July 14, 1958.

2. Natural history of the six-lined racerunner, Cnemidophorus sexlineatus. By Henry S. Fitch. Pp. 11-62, 9 figs., 9 tables. September 19, 1958.
3. Home ranges, territories, and seasonal movements of vertebrates of the Natural History Reservation. By Henry S. Fitch. Pp. 63-326, 6 plates, 24 figures in text, 3 tables. December 12, 1958.
4. A new snake of the genus Geophis from Chihuahua, Mexico. By John M. Legler. Pp. 327-334, 2 figures in text. January 28, 1959.
5. A new tortoise, genus Gopherus, from north-central Mexico. By John M. Legler. Pp. 335-343. April 24, 1959.
6. Fishes of Chautauqua, Cowley and Elk counties, Kansas. By Artie L. Metcalf. Pp. 345-400, 2 plates, 2 figures in text, 10 tables. May 6, 1959.
7. Fishes of the Big Blue River Basin, Kansas. By W. L. Minckley. Pp. 401-442, 2 plates, 4 figures in text, 5 tables. May 8, 1959.
8. Birds from Coahuila, México. By Emil K. Urban. Pp. 443-516. August 1, 1959.
9. Description of a new softshell turtle from the southeastern United States. By Robert G. Webb. Pp. 517-525, 2 pls., 1 figure in text, August 14, 1959.
10. Natural history of the ornate box turtle, Terrapene ornata ornata Agassiz. By John M. Legler. Pp. 527-669, 16 pls., 29 figures in text. March 7, 1960.

Index will follow.

Vol. 12. 1. Functional morphology of three bats: Eumops, Myotis, Macrotus. By Terry A. Vaughan. Pp. 1-153, 4 plates, 24 figures in text, July 8, 1959.

2. The ancestry of modern Amphibia: a review of the evidence. By Theodore H. Eaton, Jr. Pp. 155-180, 10 figures in text. July 10, 1959.
3. The baculum in microtine rodents. By Sydney Anderson. Pp. 181-216, 49 figures in text. February 19, 1960.
4. A new order of fishlike Amphibia from the Pennsylvanian of Kansas. By Theodore H. Eaton, Jr., and Peggy Lou Stewart. Pp. 217-240, 12 figures in text. May 2, 1960.

More numbers will appear in volume 12.

Vol. 13. 1. Five natural hybrid combinations in minnows (Cyprinidae). By Frank B. Cross and W. L. Minckley. Pp. 1-18. June 1, 1960.

2. A distributional study of the amphibians of the isthmus of Tehuantepec, México. By William E. Duellman. Pp. 19-72, pls. 1-8, 3 figs. August 16, 1960.

More numbers will appear in volume 13.

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A New Subspecies of Slider Turtle (Pseudemys scripta) from Coahuila, México

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In September, 1958, the author and two colleagues collected a large series of *Pseudemys* in small ponds and in a river in the basin of Cuatro Ciénegas, Coahuila. The specimens prove to represent a previously unrecognized subspecies of *Pseudemys scripta.* The subspecies is named in honor of Edward Harrison Taylor who has contributed more than any other person to our present knowledge of the herpetofauna of México.

Pseudemys scripta taylori new subspecies

(Pls. 9-12, Figures 1 & 2)

Holotype.—Univ. Kansas Mus. Nat. Hist., No. 46952, adult female, alcoholic; 16 km. S Cuatro Ciénegas, Coahuila, México; 6 September 1958; original number 1694 John M. Legler.

Paratypes.—A total of 52 specimens as follows (numbers or series of numbers marked with an asterisk are for specimens prepared as dry shell with soft parts in alcohol): KU 46932-4 *, 46949-51, 46953-67, 46969 (females), 46935 *, 46936-48, 46968 (males), same data as holotype, 6 to 8 September 1958; UU 3416 (male), same locality, 29 to 30 July 1959; KU 46971, 46973 * (females), 46972 (male), 46970, 46974 (juveniles), 6 mi. W Cuatro Ciénegas, 3 to 6 September 1958; IU 43585, 43587-9 (females), 43586, 43590 (males), same locality, 11 July 1958; CNHM 55655 (female), same locality, 22 August 1939; KU 46976 (female), Río Chiquito, 10 km. S Cuatro Ciénegas, 9 September 1958; UU 3415 (female), 8.5 mi. SW Cuatro Ciénegas, 1 August 1959.

Diagnosis.—A subspecies of *Pseudemys scripta* most closely resembling *P. s. elegans,* but differing from that subspecies in having: 1) extensive *black* plastral pattern, all parts of which are interconnected, covering approximately half of plastron; 2) tendency toward melanism, in large adults of both sexes, especially noticeable on posterior part of plastron; 3) cutting edge of lower jaw coarsely serrate; 4) tendency for femoral edges of plastron to be reflected ventrally, especially in males; and, 5) pectoral scute longer than gular.

Description of holotype (measurements given in Table 1).—Carapace oval in dorsal aspect, slightly narrowed behind, nearly straight across anterior margin, bluntly serrate behind; shell deep, highly arched in cross section; height of shell 53 per cent of width; surface of shell having longitudinal striations; middorsal keel weakly developed, scarcely discernible except on third central lamina; lateral margin of carapace not at all reflected, posterolateral margins flared outward; central laminae all broader than long, the first urn-shaped.

Ground color of carapace (hereinafter, colors are those of preserved specimen) dark olive; upper surface of each marginal scute having round or oval

TABLE 1. MEASUREMENTS (IN MILLIMETERS) OF THE HOLOTYPE (46952) AND NINE ADULT, TOPOTYPIC PARATYPES OF PSEUDEMYS SCRIPTA TAYLORI NEW SUBSPECIES. HEIGHT WAS MEASURED IN A VERTICAL LINE FROM THE CENTER OF THE PLASTRON.

Collection and Catalogue No.	Sex	Length of Carapace	Width of Carapace	Length of Plastron	Width of Plastral Forelobe (Humeropectoral)	Width of Plastral Hind Lobe (Mid-femoral)	Height	Width of Head
KU 46948	♂	179	127	157	71	69	69	28
KU 46941	♂	148	107	129	59	59	57	25
KU 46968	♂	139	99	116	55	54	57	25
KU 46937	♂	128	100	115	54	52	47	21
KU 46944	♂	105	82	93	46	43	38	19
KU 46932	♀	214	158	196	86	84	87	37
KU 46952	♀	202	149	186	87	86	79	33
KU 46957	♀	188	138	167	79	80	68	31
KU 46959	♀	156	118	149	71	71	70	29
KU 46962	♀	132	101	119	58	53	51	24

black mark, two such marks on each marginal of first pair; marks on margin of anterior half of carapace having pale orange-yellow borders, marks more posteriorly having indistinct borders or no border; upper surface of carapace having numerous, irregularly arranged black marks on a faint reticulum of pale lines; one or two large oval marks on each lateral scute arranged more or less vertically, other marks on laterals irregular in size and arrangement; central scutes having three to five longitudinally arranged, narrow black marks on each scute.

Ground color of plastron pale yellow, anterior half extensively marked with black along laminal seams; all plastral markings interconnected; undersurfaces of marginals on anterior half of shell having pale centers; undersurfaces of posterior marginals and posterior half of plastron solid black.

Plastron more or less evenly rounded in front, slightly indented on gular border; posterolateral free edge of plastron reflected slightly downward; posterior border of plastron having wide shallow anal notch; plastral laminae, in order of length—abdominal, anal, pectoral, gular, femoral, humeral; abdominal lamina longer than combined lengths of pectoral and humeral or humeral and gular.

Head moderately wide; snout slightly pointed in dorsal view, curving evenly backward and downward from nostrils in profile; upper jaw notched in middle, cutting edges finely and unevenly serrate, crushing surfaces having distinct ridge bearing fine denticulations but no large teeth; cutting edges of lower jaw coarsely and evenly serrate, tooth at symphysis relatively large; raised ridges of lower crushing surfaces each having low blunt tooth and many fine denticulations.

Major markings of head and neck as follows: narrow stripe beginning at posterior edge of eye and extending downward and backward (across tympanum) on side of neck to shoulder (stripe wider behind than at origin); wide stripe from lower posterior corner of eye extending downward, across mandibular articulation (and below tympanum) on throat to shoulder (wider at origin than behind); postorbital mark, four to five millimeters wide, approximately 26 millimeters long, connected to eye by narrow isthmus anteriorly and continuous with narrow stripe on upper part of neck posteriorly; stripe on mandibular symphysis widened and bifurcated posteriorly, its two branches enclosing one wide and two narrow stripes; wide stripe beginning in middle of mandibular ramus and running backward to point below mandibular articulation on each side; top of head, sides of snout, and areas between abovementioned major stripes, marked with numerous, fine, often indistinct pale lines.

Pale dorsal stripe on fleshy portion of each finger, those of second and fourth fingers continuous to mid-humeral region, those of other fingers broken on anterior face of antebrachium; upper and lower pale stripes of antebrachium joined in mid-humeral region.

Coloration of living specimens.—Ground color of soft parts dark olive to slate gray or black; ground color of carapace olive to slate gray; ground color of plastron pale yellow, markings blackish, tinged with brown in younger specimens, sooty black in most adults. Postorbital mark red; other markings on soft parts cream to buffy yellow.

Geographic range.—*Pseudemys scripta taylori* is known only from ponds, and the Río Chiquito in the basin of Cuatro Ciénegas. The discovery of *taylori* brings to six the number of valid subspecies of *scripta* known in México (*elegans, gaigeae, hiltoni, nebulosa, ornata,* and *taylori*) and to three (*elegans, gaigeae,* and *taylori*) the number known in Coahuila. My own studies of these six subspecies indicate that they are, beyond reasonable doubt, members of a single polytypic species (*scripta*). I tentatively follow Williams (1956:153) in rejecting "*cataspila*" as an invalid name.

Three specimens of *Pseudemys scripta* obtained by Robert G. Webb in the Río Chiquito at a point 8 mi. W of Nadadores, 2100 ft., where the river flows out of the basin of Cuatro Ciénegas, have many characteristics in common with *taylori,* but resemble *elegans* closely in several characters as follows: no extensive melanism; plastral markings tending to be brownish; anterior plastral markings smudgelike, isolated or nearly isolated; markings on lateral scutes tending to have vertical, linear arrangement; cutting edge of mandible weakly serrate; femoral edges of plastron not reflected ventrally; one or more fine, pale lines between two major stripes on antebrachium; gular longer than pectoral in one specimen, longer than femoral in both specimens. The nature of these specimens suggests that parts of the Río Salado drainage north and east of Cuatro Ciénegas are in a zone of intergradation between *taylori* and *elegans.* I have examined what I consider to be typical examples of *P. s.*

elegans from the region of Múzquiz (CNHM 28843-45, 55625-45), and from Don Martín Reservoir (KU 33524). These localities are, respectively, approximately 70 miles north-northeast and 100 miles east-northeast of Cuatro Ciénegas. The specimens from Múzquiz are presumably the same that Carr (1952:262) treated as ". . . *elegans-cataspila* intergrades, but with a strong leaning toward eastern *elegans*. . . ." Populations of *P. scripta* in central eastern Coahuila (between the above-mentioned localities and Cuatro Ciénegas) probably are a conglomerate of only two subspecies (*elegans* and *taylori*), not including *gaigeae* (as was suggested by Hamilton, 1947:65 and by Carr, *op. cit.*:241, map 17;262).

Specimens reported by Schmidt and Owens (1944:101) as *P. s. gaigeae* (from several localities in the region mentioned above) have been examined in the course of my study and prove to be *P. floridana texana*. A specimen reported by Shannon and Smith (1949:399; IU 4094, Hidalgo Co., Texas) as being either *gaigeae* or an *elegans-gaigeae* intergrade, has been examined and is here regarded as a typical specimen of *elegans*. I regard *P. s. gaigeae* as a subspecies of the upper Río Grande and disrupted parts of that drainage; the range of that subspecies meets that of *P. s. elegans* somewhere between the Big Bend region and Piedras Negras. In any event, the influence of *gaigeae* is not so widespread as other authors (Carr, *loc. cit.;* Hamilton, *loc. cit.;* Hartweg, 1939:3-4) have indicated.

Further collecting in the Río Salado and its tributaries east and north of Cuatro Ciénegas will be necessary before the exact range of *P. s. taylori* can be determined.

Variation.—Characteristics ascribed to the holotype pertain in general to all specimens in the hypodigm, except as noted below. The postorbital mark is in contact with the eye on one or both sides in 46 per cent of the specimens (narrowly separated from eye in remainder) and is in contact with a neck stripe (on one or both sides) in 35 per cent of the specimens. The pattern of the antebrachium is as shown in Fig. 2 in all specimens except that the thin lateral stripe is obliterated by melanism in older specimens of both sexes. The lateral edges of the posterior plastral lobe are reflected downward, at least slightly, in all but one specimen (an adult, kyphotic female). The first central lamina is straight-sided in juveniles and becomes urn-shaped only in adults. The relative height of the shell tends to increase with a general increase in size in both sexes.

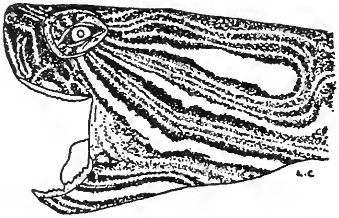


FIG. 1. *Pseudemys scripta taylori* new subspecies: left side of head, female paratype (KU 46933), × 1.

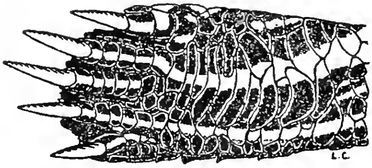


FIG. 2. *Pseudemys scripta taylori* new subspecies: anterior view of left antebrachium, female paratype (KU 46934), × 1.

Comparisons.—Of the five other subspecies of Mexican *P. scripta* mentioned above, three subspecies (*gaigeae, hiltoni,* and *nebulosa*) form a natural group herein referred to as the *gaigeae* group. *Pseudemys s. taylori* is distinguished from members of the *gaigeae* group by elongate, red postorbital mark (yellow or orange in the *gaigeae* group), extensive black plastral pattern (narrow—or if wide, brownish—in *gaigeae* group), and serrate lower jaw (nearly smooth in *gaigeae* group).

The subspecies *P. scripta taylori* differs from *P. scripta elegans* as indicated in the following compartive list of characteristics:

P. s. taylori	*P. s. elegans*
1. Extensive black plastral pattern, all parts of which are interconnected. Plastral pattern partly obliterated by melanism in old individuals of both sexes.	1. Plastral pattern consisting of separate brown smudges (at least anteriorly). Plastral pattern obliterated by melanism only in adult males.
2. Markings of carapace in form of indistinct ocelli.	2. Markings of carapace having linear and vertical.
3. Cutting edge of mandible serrate.	3. Cutting edge of mandible smooth.
4. Foreclaws of mature males unmodified.	4. Foreclaws of mature males greatly elongated.
5. Gular shorter than pectoral (91 per cent of specimens), gular and femoral subequal.	5. Gular longer than pectoral (90 per cent of specimens) and longer than femoral (all specimens).
6. Shell relatively higher, posterior lobe of plastron relatively narrower (Fig. 3).	6. Shell relatively lower, posterior lobe of plastron relatively wider (Fig. 3).
7. Lateral edges of posterior plastral lobe reflected downward.	7. Lateral edges of posterior plastral lobe unmodified.

Four specimens of *P. s. ornata* (MCZ 46392-3, 46397, 46400, two adult females and two adult males) from the Río Soto la Marina drainage of Tamaulipas differ from *P. s. taylori* as follows: plastral pattern diffuse and brownish, not black; gular longer than pectoral; cutting edge of lower jaw only slightly serrate; stripe on mandibular symphysis isolated, not joined with ventral neck stripes to form inverted Y; postorbital stripe (yellow in preservative) connected to eye by narrow isthmus and continuous with neck stripe to shoulder.

In *P. s. taylori* there is an obtuse ridge or prominence across the bridge, on a line joining the free lateral edges of the plastron; the area between the ridges is nearly flat. The bridge forms a distinct plane on each side between the mentioned ridge and the outer edges of the marginals. In cross section this plane forms an angle of 30 to 45 degrees with the horizontal plane of the plastron. The higher bridge and deeper shell of *taylori* result in a slightly higher center of gravity in this subspecies than in the specimens of *elegans* and *ornata* I have examined. In the two subspecies last named the longitudinal ridges on the plastron are indistinct or wanting and the bridge forms a lesser angle with the horizontal plane of the plastron.

The largest female of *taylori* (218 mm.) is shorter by some 30 mm. than the smaller female in the series of *ornata* from Tamaulipas whereas the largest male of *taylori* (179 mm.) is shorter by some 80 mm. than the smaller male from Tamaulipas. *Pseudemys s. taylori* probably is smaller, on the average, than either *elegans* or northern populations of *ornata.*

There seems to be no reliable published record of the color of the postorbital mark in living examples of *P. s. ornata* from Tamaulipas. Williams (1956: 147, 154) indicated that this color may be red or yellow for Mexican and Central American populations of *ornata* in general and Günther (1885: Pl. 6 b) indicated that the color was yellow in *Emys cataspila;* however, both of the observations mentioned were presumably based on preserved rather than living specimens. The postorbital marks of a live specimen of *ornata* (KU 40131) from southern Veracruz were yellowish to buffy with a pinkish tinge anteriorly (*fide* notes of Robert G. Webb and a color photograph by him).

Natural history.—Specimens of *P. s. taylori* were caught in hoop nets in clear deep pools and in the Río Chiquito. No specimens were collected or observed in marshy situations where the water

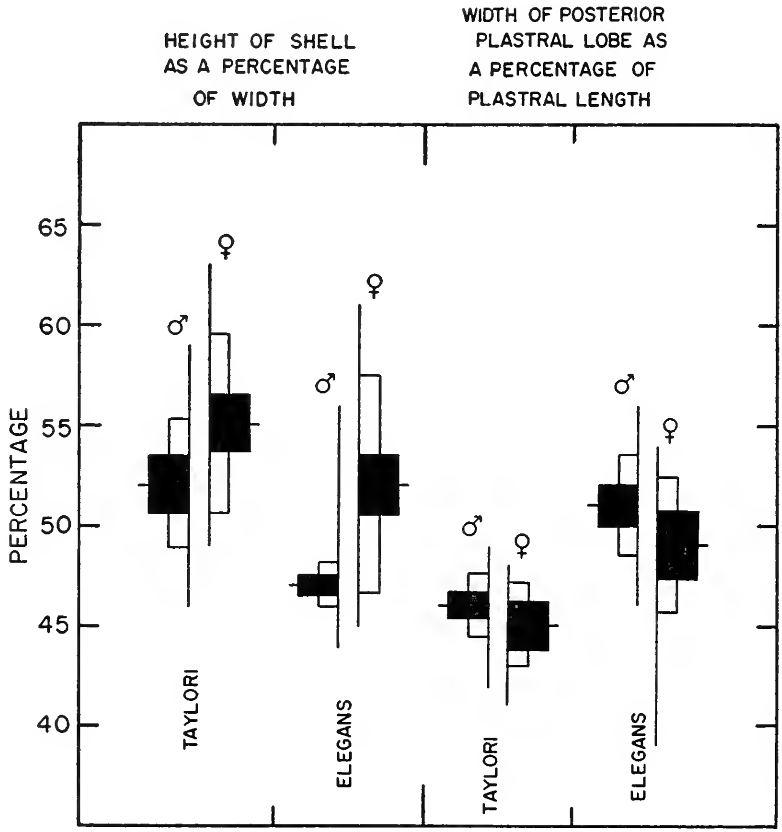
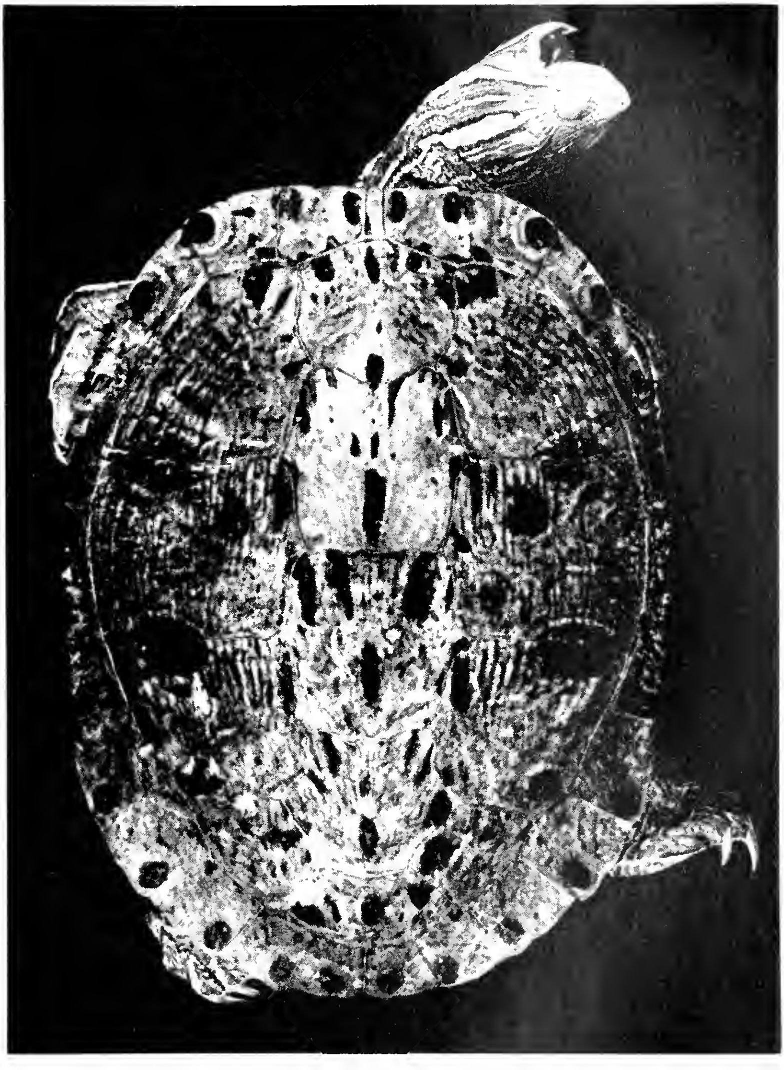


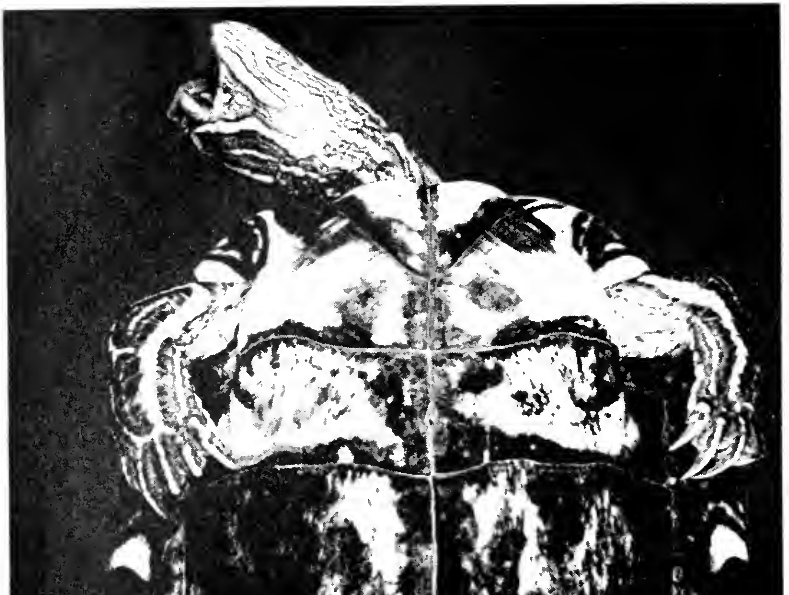
FIG. 3. Relative height of shell (expressed as a percentage of width) and relative width of posterior plastral lobe (expressed as a percentage of plastral length) in two subspecies of *Pseudemys scripta*. The data presented are for 62 specimens (40♀, 22♂) of *P. s. taylori* and 37 specimens (13♀, 24♂) of *P. s. elegans*. Horizontal and vertical lines represent the mean and range, respectively, whereas open and solid rectangles represent one standard deviation and two standard errors of the mean, respectively.

PLATE 9



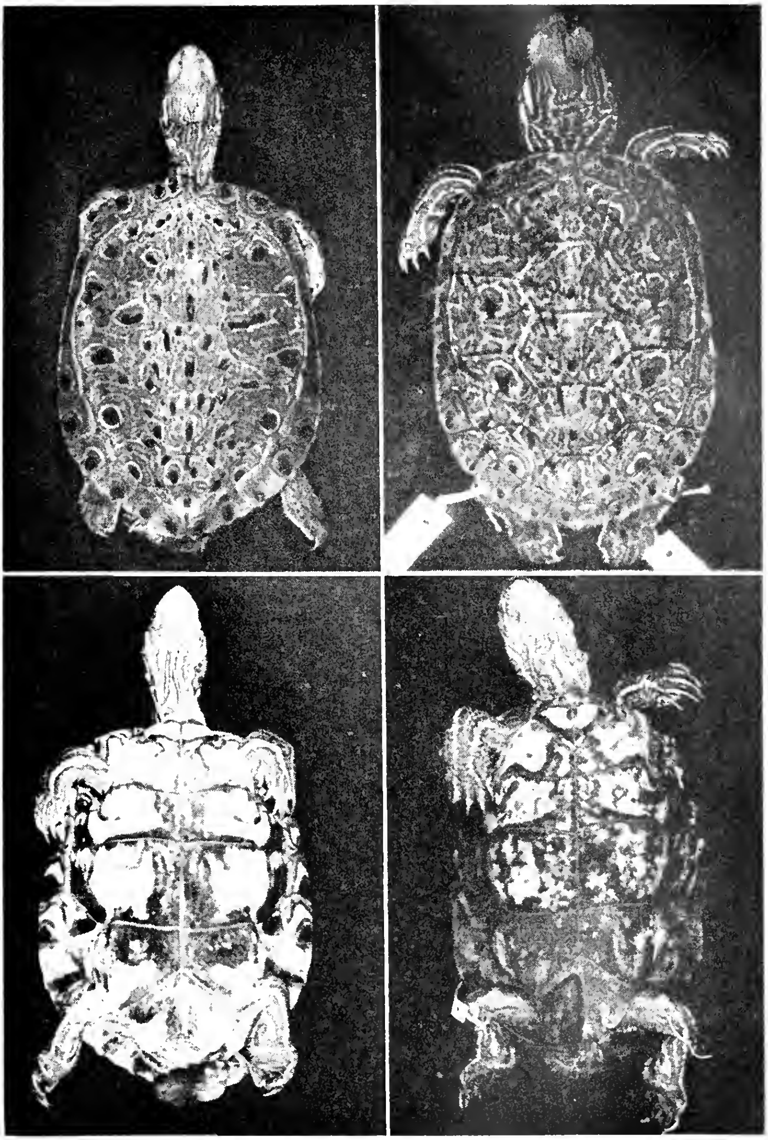
Pseudemys scripta taylori new subspecies: dorsal view of holotype (KU 46952), approximately 11/16 natural size.

PLATE 10



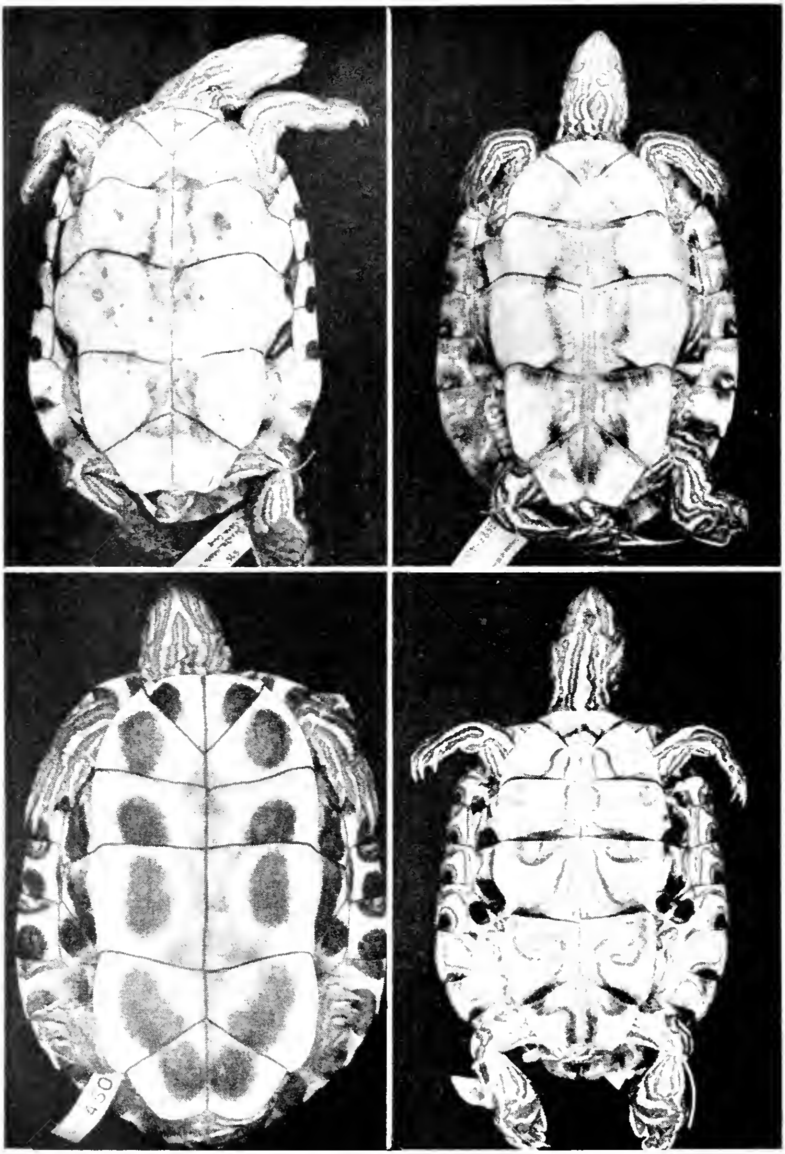
Pseudemys scripta taylori new subspecies: ventral view of holotype (KU 46952), approximately 11/16 natural size.

PLATE 11



Paratypes of *Pseudemys scripta taylori* new subspecies: *Left*—dorsal and ventral views of KU 46943, male, 16 km. S Cuatro Ciénegas, × ⅜; *Upper right*—KU 46974, juvenile, 6 mi. W Cuatro Ciénegas, × ⅚; *Lower right*—KU 46968, male, 16 km. S Cuatro Ciénegas, × ⅜.

PLATE 12



Ventral views of four subspecies of *Pseudemys scripta: Upper left—P. s. ornata* (KU 40131♀), Río Playa Vicente, San Andrés Tuxtla, Veracruz, × ⅓; *Upper right—P. s. gaigeae* (IU 43583♀), 1 mi. E La Cruz, Chihuahua, × ⅜; *Lower left—P. s. elegans* (CNHM 55627♂), Múzquiz, Coahuila, × ⅔; *Lower right—P. s. taylori* new subspecies (KU 46970 juvenile), paratype, 6 mi. W Cuatro Ciénegas, Coahuila, × 11/16.

was shallow or stagnant. Individuals were seen only near dusk and in early morning when a number floated just below the surface with only their heads showing. They were never seen on land during our short stay in the basin. The few stomachs that were opened contained vegetable material. In terms of number of specimens trapped, *P. s. taylori* was the most abundant turtle in pools at and near the type locality (Webb and Legler, 1960).

Relationships and phylogeny.—The basin of Cuatro Ciénegas now drains, via the Río Salado, into the lower Río Grande. Brief descriptions of habitats and topography in the basin are given by Gilmore (1947:148-150, fig. 2) and Webb and Legler (1960). In the more northern parts of the Salado drainage (for example, in the Río Sabinas near Múzquiz) slider turtles are typical *P. s. elegans.* Assuming that conditions which permit genetic exchange between populations of turtles in the Salado drainage system differ in no major respect from conditions in other parts of the range of *Pseudemys scripta,* it is logical to suppose that the differentiation of *P. s. taylori* at Cuatro Ciénegas was preceded by the isolation of a population in that basin.

The Río Chiquito drains through a narrow gap in the northeastern end of the basin of Cuatro Ciénegas. Interruption of this stream would effectively isolate aquatic habitats in the basin.

It is here proposed that *P. s. taylori* is a relict of an earlier, lower Río Grande stock, part of which became isolated in the basin of Cuatro Cíenegas in postpluvial times. The morphological similarity of *P. s. taylori* and *P. s. elegans* indicates that both were derived from this parent stock; similarity of both subspecies to populations of *P. s. ornata* in Tamaulipas suggests that the latter subspecies may also be a derivative of the mentioned stock of the lower Río Grande.

The proposed former isolation of the basin of Cuatro Ciénegas is supported by evidence found in studies of other turtles in the basin. Of the four kinds of turtles known to occur there (*Terrapene coahuila, P. s. taylori, Trionyx spinifer emoryi,* and *Trionyx ater*), all but *T. spinifer* seem to be endemic. These three kinds comprise a graded series, in regard to their degree of differentiation from closest known relatives, as follows: 1) *Terrapene coahuila* is morphologically the most generalized and primitive of living box turtles; the species is unique in its highly aquatic mode of life (see Legler, 1960:532-534, for brief discussion of relationships within genus *Terrapene*); 2) *Trionyx ater* seems to represent a relict population of pre-*Trionyx spinifer* stock; presumably, *spinifer* has reinvaded the basin of Cuatro Ciénegas in relatively recent times and, as noted above, *spinifer* and *ater* now occur sympatrically (at least in a geographic sense) in the basin (Webb and Legler, *op. cit.*); and, 3) evidence presented above suggests that *P. s. taylori* intergrades with *P. s. elegans* outside the basin.

The three endemic populations of turtles at Cuatro Ciénegas therefore, differ by varying degrees from their closest living relatives. This variation in degree of difference possibly results from varying periods of isolation. Probably the basin of Cuatro Ciénegas has been isolated from, and reconnected to, the lower Río Grande drainage at several times in the past. The relationships of fishes in the basin, now under study by other workers, also suggest that the basin was isolated more than once.

Remarks.—Local names for the above-mentioned localities in the basin of Cuatro Ciénegas are as follows: Anteojo (6 mi. W Cuatro Ciénegas); El Mojarral (8.5 mi. SW); and Ojo de Agua de Tío Candido, on Rancho Orozco (16 km. S). The Río Chiquito is referred to by some natives as "Río Colorado" and by some as "Río Salado." The local name for *P. s. taylori* is *tortuga negra* (the name is used also for *Terrapene coahuila*).

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Comparative materials examined (total of 135 specimens).—*P. s. elegans* (52 specimens): KU 2897-8, 3195, 18337, 18341, 18345, 18347, 18364, 45027-31, 45033, 46750, 46863, and John M. Legler 1394 and 1435, various localities, Kansas; KU 16400, Howard Co., Texas; KU 39983-4, 8 mi. N and 2 mi. W Piedras Negras, Coahuila; KU 33525, 33527-9, La Gacha, Coahuila; CNHM 28843-5, 55625-45, Rancho las Ruscias, Múzquiz, Coahuila; KU 39982, 2 mi. S and 3 mi. E San Juan de Sabinas, Coahuila; KU 33524, Don Martín Reservoir, Coahuila; *P. s. elegans* × *taylori* (3): KU 53785-7, 8 mi. W. Nadadores, Coahuila; *P. s. gaigeae* (39): MCZ 54724, Elephant Butte Reservoir [Sierra or Socorro Co.], New Mexico; KU 51158-61, 51202-3, Lajitas, Brewster Co., Texas; KU 51162-6, 51204-6, 51315, 1 mi. NW Ojinaga, Chihuahua; KU 33884, 51167-72, 51207-20, 3 mi. N and 5 mi. E Meoqui, Chihuahua; IU 43583-4, La Cruz, Chihuahua; *P. s. ornata* (9): MCZ 46392-3, Río Purificación, Rancho Sta. Ana, Tamaulipas; MCZ 46397, E of Güémez, Tamaulipas; MCZ 46400, Jiménez, Tamaulipas; KU 40161-2, Alvarado, Veracruz; KU 40131, San Andrés Tuxtla, Veracruz; V. E. Thatcher 98, 15 mi. N Teapa, Tabasco; KU 40139, Cantemo[c], Tabasco; *P. s. taylori* (23 in addition to type series): KU 51438, 51442, 53788-53801 topotypes; KU 53802-5, 8.5 mi. SW Cuatro Ciénegas, Coahuila; KU 51439-41, 10 km. S Cuatro Ciénegas, Coahuila; *P. floridana texana* (10 from Coahuila): KU 39985, 2 mi. W Jiménez; CNHM 55654, Allende; CNHM 55646, Cd. San Juan; CNHM 55648, Hermanas; CNHM 55649-53, Lampacitas; KU 33526, Don Martín Reservoir.

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BY

HENRY S. FITCH

UNIVERSITY OF KANSAS
LAWRENCE
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3. The silky pocket mice (Perognathus flavus) of Mexico. By Rollin H. Baker. Pp. 339-347, 1 figure in text. February 15, 1954.
4. North American jumping mice (Genus Zapus). By Phillip H. Krutzsch. Pp. 349-472, 47 figures in text, 4 tables. April 21, 1954.
5. Mammals from Southeastern Alaska. By Rollin H. Baker and James S. Findley. Pp. 473-477. April 21, 1954.
6. Distribution of Some Nebraskan Mammals. By J. Knox Jones, Jr. Pp. 479-487. April 21, 1954.
7. Subspeciation in the montane meadow mouse, Microtus montanus, in Wyoming and Colorado. By Sydney Anderson. Pp. 489-506, 2 figures in text. July 23, 1954.
8. A new subspecies of bat (Myotis velifer) from southeastern California and Arizona. By Terry A. Vaughan. Pp. 507-512. July 23, 1954.
9. Mammals of the San Gabriel mountains of California. By Terry A. Vaughan. Pp. 513-582, 1 figure in text, 12 tables. November 15, 1954.
10. A new bat (Genus Pipistrellus) from northeastern Mexico. By Rollin H. Baker. Pp. 583-586. November 15, 1954.
11. A new subspecies of pocket mouse from Kansas. By E. Raymond Hall. Pp. 587-590. November 15, 1954.
12. Geographic variation in the pocket gopher, Cratogeomys castanops, in Coahuila, Mexico. By Robert J. Russell and Rollin H. Baker. Pp. 591-608. March 15, 1955.
13. A new cottontail (Sylvilagus floridanus) from northeastern Mexico. By Rollin H. Baker. Pp. 609-612. April 8, 1955.
14. Taxonomy and distribution of some American shrews. By James S. Findley. Pp. 613-618. June 10, 1955.
15. The pigmy woodrat, Neotoma goldmani, its distribution and systematic position. By Dennis G. Rainey and Rollin H. Baker. Pp. 619-624, 2 figures in text. June 10, 1955.

Index. Pp. 625-651.

(Continued on inside of back cover)

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CONTENTS

DESCRIPTION

BEHAVIOR

REPRODUCTION

GROWTH AND DEVELOPMENT

FOOD HABITS

DEFENSE, ESCAPE AND MORTALITY FACTORS

RELATION TO MAN

THE VENOM AND BITE

INTRODUCTION

In 1948 when ecological studies were initiated on the newly created University of Kansas Natural History Reservation, the copperhead was one of the first species that attracted attention as meriting intensive investigation. As an abundant predator on small vertebrates, including both those that are primary consumers of the vegetation and those of higher trophic levels, it was recognized as a key animal in the local ecosystem.

Despite persistent effort to study the copperhead, progress was slow, especially in the early stages of the investigation. Copperheads were rarely seen engaged in their normal activities, and even when such individuals were found, observing them proved to be remarkably unrewarding. A copperhead found by chance usually lay motionless for long periods, either having "frozen" in the usual reaction to any alarm, or merely resting—the sluggish behavior that is characteristic of the species. Attempting to observe such a snake severely tried the patience of the investigator. When the snake finally began to move, it might soon be irretrievably lost because of the perfection with which it blended with its background, and the dense concealing vegetation and other cover in the situations frequented.

In the summer of 1949 cylindrical wire funnel traps set for lizards at the edges of rock outcrops in the "Rat Ledge" area caught several copperheads, and many more of these snakes were trapped in similar situations in autumn of the same year. Thereafter, each autumn, trap lines were maintained in rock ledge habitat and copperheads were obtained in numbers at that time of year but not at other seasons. In 1957 trap lines were established in a variety of habitats not previously sampled, and this trapping was continued on a larger scale in 1958 and 1959. In these three years copperheads were obtained in large numbers throughout the season of their activity.

The present report is based primarily upon records obtained on the 590-acre University of Kansas Natural History Reservation, in the northeastern corner of Douglas County, Kansas, and on the adjacent 160-acre Rockefeller Experimental Tract. Including a few miscellaneous records, such as those of snakes found dead on county roads, and of young born dead in captivity, a total of 1532 individual copperheads obtained from the Reservation or immediately adjacent areas were recorded a total of 2018 times between July 1, 1948, and November 9, 1959. Supplemental information was obtained from numerous other copperheads collected or observed elsewhere in eastern Kansas, notably from large series taken near La Cygne by Vernon Mann, who kindly permitted me to examine the live snakes in his possession from time to time.

Despite the rapid accumulation of data during the later years completion of the study was long delayed because of seeming inadequacies or inconsistencies in the information obtained. The information gained from marked copperheads recaptured after substantial intervals provides the core of this report and is the main basis for conclusions regarding movements, growth, longevity, and age distribution. However, such records of recaptured individuals were sparse in the early years of the study, and constituted a small minority even in my field work in 1959. Hence, the information obtained concerning some phases of the natural history is scanty and the conclusions drawn from it are tentative.

Because the copperhead's range is in parts of the United States longest settled and most densely populated, the species figures prominently in folklore and much has been written concerning it, both in scientific and popular literature. However, most published references to copperheads are brief and casual. Although 142 years have elapsed since the publication of Rafinesque's (1819) "Natural History of *Scytalus cupreus*, or the Copper-head Snake" no thoroughgoing account of the species' natural history and ecology has been made heretofore. Oliver (1958) has published an excellent brief summary of the literature, with some new information. Especially noteworthy contributions to knowledge of the copperhead are those of Gloyd and Conant (1943) concerning taxonomy, Gloyd (1934), Smith (1940) and Allen (1955) concerning reproduction, Uhler, Cottam and Clarke (1939), Clark (1949) and Hamilton and Pollack (1955) concerning food habits, and Minton (1951, 1954, 1956) concerning the venom. Also deserving of mention is Klauber's (1956) monumental monograph of the rattlesnakes, which has shed much light on the biology of the pit vipers, and on snakes in general, and has been a frequent reference source in the course of my work.

In preparing the present report I have examined all available publications pertaining to copperheads, and have drawn freely on

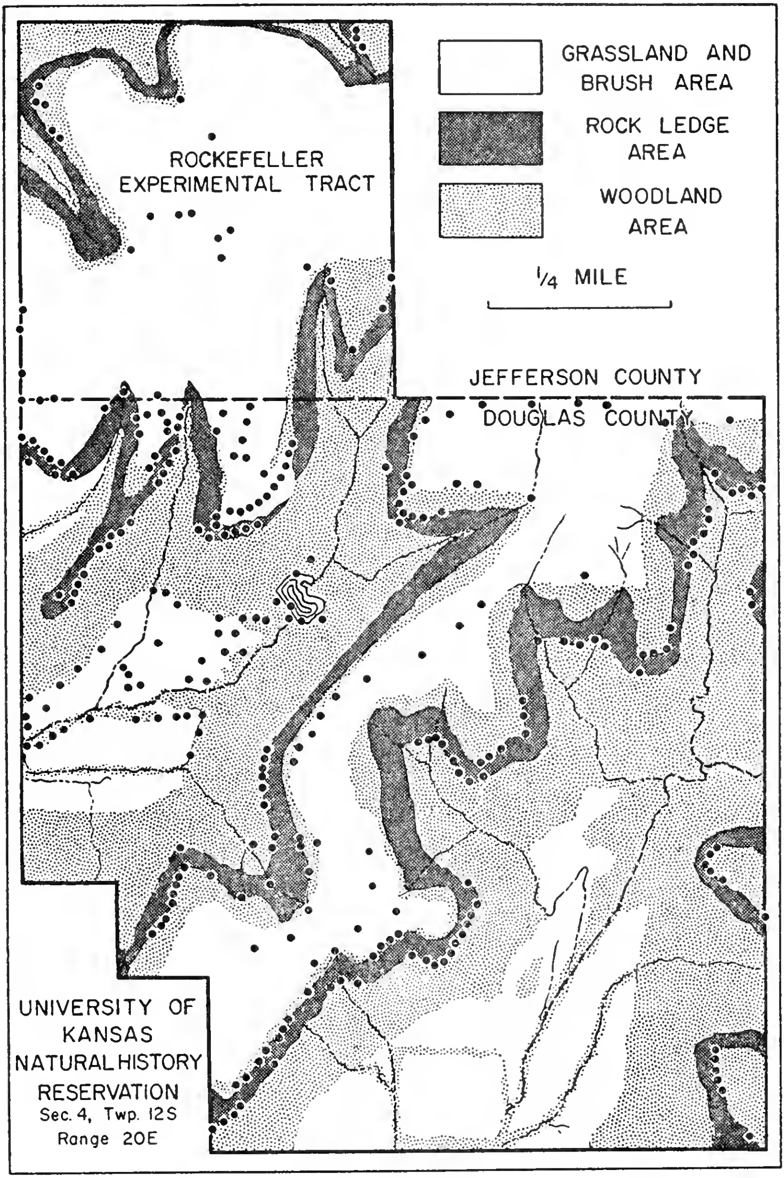

FIG. 1. Map of area approximately six miles north-northeast of the University of Kansas campus at Lawrence, where field work on copperheads was concentrated—the combined University of Kansas Natural History Reservation and Rockefeller Experimental Tract. Each large dot shows a location where at least one copperhead was captured.

these sources for supplementary or comparative material. For certain phases of the copperhead's biology that were marginal to my study or were already rather thoroughly investigated (for example, the venom and the bite) the material here presented is based mainly or entirely on published literature.

The present report will be of interest chiefly to specialists, but, it is hoped, will also have some practical value. The copperhead affects human affairs in various ways, as by destroying harmful rodents, by destroying certain beneficial animals including lizards and toads, and occasionally by injuring or even killing humans and domestic animals by its venomous bite. Its greatest importance is probably the devastating psychological effect that its appearance or suspected presence creates in many persons. It is to be hoped that a better understanding of its habits and limitations may eventually help to dispel this unreasoning fear. Also, the information here assembled concerning movements, food habits, population turnover, and seasonal habits provides a background essential for the planning of control operations. Certainly wholesale control operations against the copperhead are neither practicable nor desirable, but locally, for example in suburban communities where high populations of copperheads in remaining blocks of woodland constitute a hazard to small children, control may be both necessary and feasible.

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In the early stages of the study Drs. Richard E. Freiburg, Richard B. Loomis, and Dennis G. Rainey, then graduate students engaged in field work on the Reservation contributed many specimens and records, as did John A. Knouse, Anthony N. McFarland, Kenneth E. Shain and Robert B. Wimmer, in the later stages.

Mr. Vernon Mann, professional snake collector of La Cygne, Kansas, kindly co-operated in allowing me to examine the live copperheads in his collection and to collect their scats and shed fangs. Mrs. Norma Rothman, Dr. Joseph P. Kennedy and Dr. Bayard Brattstrom generously contributed original field notes and Dr. Kennedy also contributed food habits material. Mr. and Mrs. Harold Hedges of Kansas City, Kansas, contributed a fine series of live copperheads. Mr. Ian D. W. Sutherland of Tulane University contributed notes and photographs concerning the courtship of copperheads in captivity. I am

especially indebted to Dr. William Degenhardt who spent many hours in the field with me when I visited Big Bend National Park in July, 1957, taking me to several remote areas where copperheads had been collected in the Park, and drawing on his excellent knowledge of the region to clarify various matters regarding its physiography and ecology. Mrs. Eleanor E. Buckley of Wyeth Laboratories, Inc., kindly provided me with information concerning the improved antivenin serum and referred me to important recent literature concerning the treatment of snake-bite. Drs. Frederick H. Dale and William H. Stickel kindly checked the files on food-habits in the U. S. Fish and Wildlife Service on my behalf for records of predation on copperheads by birds and mammals.

METHODS

Copperheads were obtained chiefly by means of live-traps of the same general style that I have already described (Fitch, 1951:77). These cylinders of galvanized hardware cloth wire, of quarter-inch mesh, were one foot to two feet in length (usually 15 or 18 inches), and most of them were approximately seven inches in diameter. At one end of the trap, or at both ends, an entrance funnel was inserted. The large end of the funnel was approximately twice the diameter of the trap, and the opening at the small end was approximately an inch in diameter. These traps were modified and improved in various ways in the course of the study. The valve-type doors of transparent cellulose acetate, which were used in the early model were eventually abandoned; to discourage exit of the trapped snake, cut ends of the wire were shaped into a circle of inward-projecting prongs. A heavy wire pin nine inches long, with a sharp point at one end and with the other end bent into the shape of a hook, was used to lock the funnel in place on the end of the trap. The pin was curved in a bow shape. It was thrust through the trap and funnel approximately an inch from the end of the trap, with the convexity outward. Before the terminal hook engaged the wire of the trap's side, the pin was rotated through 180 degrees, with the result that the funnel was drawn firmly into position against the trap. Some traps were reinforced by attaching a heavy wire ring to the edge of the hardware cloth at the trap's opening and attaching a ring of the same size to the funnel. When the trap was set, with the reinforcing rings of the funnel and the trap's end in contact, it was almost impregnable to predators. At times, especially in autumn, raccoons, skunks, and other predators tore open the traps not so reinforced, to eat the animals that had been caught in them. In most instances grasshoppers, beetles, frogs or mice that wandered into the traps attracted these predators. It is not known whether any trapped snakes were killed by the raiders. Once a young copperhead, partly eaten was found beside a trap that was broken open, but in this instance the snake had already been killed by freezing. Reliance was placed upon the strategic placement of the traps, and no bait was used. However, various small animals that wandered into the traps may have served occasionally as attractants to snakes.

The wire funnel traps were sometimes used with a funnel in each end, at other times were used with a funnel in one end and a plug in the other. The plugs consisted of wire cones or of metal disks (ends of "tin" cans) with wire loops attached, and were locked into place with pins in the same manner as the funnels.

Usually funnels were used in each end in autumn when traps were set along hilltop rock outcrops. Sites for the sets were carefully selected, where vertical rock faces presented barriers, with the expectation that snakes would travel along the base of the outcrop either in contact with the rock or adjacent to it. In placing the trap, care was used to shape the outer edge of the funnel, molding it against the ground surface and the rock face so that no space sufficiently large to permit a snake to squeeze under or past the trap remained (Plate 13, fig. 2).

In summer when the snakes had dispersed from the rock ledges where hibernation occurred, trapping could be carried on most effectively in fields, thickets and the edges of woodland. In the absence of natural barriers, drift fences were erected to direct snakes into the funnel entrances. Ten-inch boards set up on edge and supported by small wooden stakes, by rocks or by shrubby vegetation were utilized as drift fences. In earlier trapping, two such boards were set up to form a V converging into the funnel, at each end of the trap. Later it was found more effective to set up several boards end-to-end in a single straight fence, with a trap at each end. Used in this way each trap had only one entrance, and the opposite end was closed with a plug. The continuous drift fences were judged to be more effective than the double V arrangement because both sides of the drift fence functioned to steer snakes toward the traps.

The traps were seldom checked oftener than once per day, or less often than once per week, but no regular schedule was maintained for checking them. Frequency of checking was influenced by the weather, the productiveness of the trap lines from time to time, and the amount of time available for this purpose. Traps set at the hilltop rock outcrops were held in place by flat rocks, placed beside them and over them. The traps set in summer away from woodland were always placed in sites beneath a tree or bush, or some other shelter that provided shade for most of the day, especially the hotter part of it. As further protection piles of straw or other vegetation were placed on the traps.

Ordinarily the snakes trapped were processed in the field and released without removal from the site. Techniques varied somewhat according to the circumstances. The plug or funnel was removed from one end of the trap and the snake was shaken into a cloth bag and weighed on spring scales of 500-gram or 250-gram capacity. Weights obtained in the field were accurate within a range of one or two grams. After weighing, the snake was emptied out of the bag and almost invariably it coiled on the defensive rather than attempting to escape. It was then held down, caught by hand, measured, and examined. Special technique was of course necessary to avoid the venomous bite of the snake while catching, handling and releasing it. In either catching or releasing a copperhead I always held down its head with a stick or ruler to prevent it from striking while my hand was within its reach. In picking up the snake I grasped it firmly just behind the head with the forefinger of my left hand around its neck, and my thumb holding it firmly in place. This grip was maintained until the snake was released. While holding the snake in this manner it is important to keep the forefinger back away from the chin, as the snake may bite through its own lower jaw. In handling captive copperheads in the laboratory I often employed metal bottle tongs to grasp them. Although these tongs were only eight inches long, they provided sufficient reach to permit grasping of a copperhead of normal size, so long as a frontal approach was avoided. In the field I often carried longer metal tongs and used them to remove copperheads from traps without moving the latter from their position. For measuring, the snake was held suspended vertically and a steel tape, graduated in millimeters, was held against it with the "zero" mark on a level with the tip of the snake's snout, and the tape dangling parallel with the snake. Grasping the snake by the base of the tail with my right hand, I exerted steady downward pressure to stretch the body out full length. At first the snake usually would resist, but soon it would tire, momentarily at least, and its body would be extended full length against the tape, permitting a reading of snout-vent-length to the nearest millimeter. Tail-length was then recorded by holding the tail against a plastic ruler with the tip on the zero mark. The snake's mouth was forced open with forceps or a small stick, and the fangs were examined. Loose fangs that were being shed were removed, wrapped in paper, and labelled. Sex was determined by probing the hemipenial invagination in the base of the tail, with a loop of fine wire, or with the semi-rigid but soft ended shaft of a slender green stem of grass or other vegetation.

Every live copperhead that was examined was palpated for detection of food in the stomach. Objects detected were forced forward into the mouth, to be identified. To force a snake to disgorge I grasped it with my left hand just behind the head and my right hand at mid-body, exerting pressure forward and upward against any suspected food object. Usually such objects slipped forward easily through the gullet and could be examined without injuring the snake. Relatively few food records were obtained from stomach items, only 67 in 2018 examinations of snakes. That only approximately 3.3 per cent of the newly caught copperheads were found to have food in their stomachs can be attributed largely to the fact that a high proportion of them were taken in autumn along the rock ledges. Snakes preparing to hibernate are less inclined to feed than others. Even the individuals caught at other times are perhaps those least likely to have fed recently, since after feeding they are sluggish and tend to stay in sheltered places. The hungry snakes engaged in active prowling are most likely to be caught in traps or found in the open.

Throughout the course of my field work feces were collected from time to time, from snakes that defecated while they were in traps, bags, or cages, or while they were being handled. In 1957 it was discovered that in snakes containing food too well digested to be palpated from the stomach, fecal material could almost always be palpated from the anus. Often the hindquarters of a partly digested animal were palpated from the stomach, and parts of the same animal were found in the scat collected at the same time. In fact, if a snake had food anywhere in the digestive tract, a sample usually could be obtained and identified. A total of 315 fecal samples were collected on the Reservation.

At the most, a scat was only a few cubic centimeters in bulk. Scats collected were wrapped in absorbent tissue paper or paper towel, labelled with the date, the location, and the scale formula of the individual snake. Each scat was soaked for a day or more in a detergent solution, then rinsed, dried on a paper towel, and transferred to a cellophane envelope. The contents of each envelope were examined under a dissecting microscope and compared with collections of reference material. Mammalian material was identified chiefly from hairs. The length, diameter, shape in cross-section, taper, and coloration of hairs were in varying degrees diagnostic of the species. In some instances the cell pattern, under high powered magnification, provided useful characters. Because most of the scat material was from the Reservation where the mammalian fauna was already well known, and the number of species of a size that could be swallowed by a copperhead was small, identification was much simplified. Greatest difficulty was experienced in separating species of the same genus. The voles, *Microtus ochrogaster* and *M. pinetorum* could be identified most readily by examining the hair without magnification. Two species of *Peromyscus* were recorded but most identifications in this genus were made merely as "*Peromyscus* sp." Doubtless in most of these instances the animal eaten was the wood mouse (*P. leucopus*) since this is one of the most abundant mammals over most of the Reservation, and its habitat requirements correspond more closely with the copperhead's than do those of the deer mouse (*P. maniculatus*) which is relatively scarce and localized. No attempt was made to distinguish between the two species of harvest mice occurring on the area, but most or all occurrences in scats probably were of the common species, *Reithrodontomys megalotis.*

Because identification was made from hairs there was no indication of the number of individuals of the same species represented in a scat. It is therefore assumed that each occurrence represents a single animal. However, of the eleven copperheads found to contain prairie voles in their stomachs, one had eaten four voles, a female and her three young. Probably other multiple feedings went undetected in the identification of prey from scats. The importance of voles, especially, in the diet thus tends to be minimized. Also, in some instances the hair of one species of mammal being more abundant or more conspicuous, probably masked that of another kind in the same scat and caused it to be overlooked. Hair of harvest mouse or wood mouse associated with that of a vole, for instance, or hair of least shrew associated with that of short-tailed shrew would be difficult to recognize.

Reptiles were identified chiefly from scale material. Size, shape, presence or absence of keels, pits, and terminal notches provided distinctive combinations of characters by which the local genera, at least, could be readily distinguished. Bird material was represented only by feathers, and these were so matted and bedraggled that they provided little indication of the kind of bird unless they were of distinctive coloration. The insects that were secondary food items were usually in fragmentary condition, so that identification to species was impractical, but some of the cicadas were more nearly intact than any other items found in the scats.

The residual material in scats consisted of hard parts, chiefly integumentary structures such as hair, scales, feathers and fragments of chitin. Bones and even teeth were largely disintegrated by the digestive juices, but remains of them were often found and sometimes they were nearly intact when embedded in wads of fur or other material that partly protected them from dissolution. The fangs and other teeth of the copperheads themselves were often found in the scats and are more resistant than the teeth of other animals. Occasionally an entire foot of a lizard or mouse was found nearly intact. The thoroughness of digestion seemed to be somewhat proportional inversely to the bulk of the meal. Chitin was found to be relatively resistant to digestion, with the result that the insects eaten were better represented than the vertebrates.

Although certain large insects, chiefly cicadas and large caterpillars are eaten regularly, many of the insect remains found in scats were of small kinds which almost certainly did not represent primary food items. Small ants (*Crematogaster* and others) were found in 14 scats. Often they were intact and were represented by many individuals. The narrow-mouthed toad (*Gastrophryne olivacea*) is abundant on the Reservation and is known to feed on ants of this type almost exclusively (Fitch, 1956:301). Among the 67 prey items found in stomachs the narrow-mouthed toad comprised six per cent, but amphibians are so completely digested that ordinarily no recognizable remains can be found in scats. The 14 occurrences of ants (in varying quantities) in scats were therefore all listed as instances of predation on *Gastrophryne* although in most instances no remains of the toad itself were distinguishable. If the ratio of narrow-mouthed toads to other kinds of prey is representative for the items found in stomachs, some 31 occurrences should have been recorded in scats. Perhaps some were missed because they did not have sufficient food in their stomachs to leave noticeable residue in scats.

Other insect material was in much more fragmentary condition than the remains of cicada, caterpillar and ant, and most such occurrences probably were secondary. Of 39 occurrences of insects seven were identified as beetle. Associations were nearly always with small insectivorous vertebrates: 7 with *Cryptotis*, 7 with *Eumeces*, 6 with *Peromyscus*, 5 with *Blarina*, 5 with *Reithrodontomys*, 4 with *Microtus*, 2 with *Ophisaurus*, and one each with *Microtus*, *Sylvilagus*, *Terrapene*, *Coluber* and "bird." The last three were all in the same scat. Also, 6 of the *Eumeces*-insect occurrences, 3 of *Reithrodontomys*-insect, 3 of *Cryptotis*-insect and 2 of *Microtus*-insect were in association with other small vertebrates that are potential insect eaters. Six insect occurrences were not associated with vertebrate remains. In these instances, in the rabbit-insect association, and probably in some of the other occurrences, it seems most likely that the insects were in the digestive tract of an amphibian eaten by the copperhead and completely digested by it. These problematical occurrences of insects were tentatively assigned to the leopard frog (*Rana pipiens*) since this frog was found among the items identified from stomachs but presumably would have been completely digested and could not have been represented in scats except by the secondary prey items from its own digestive tract.

In the later stages of the study many copperheads were tested for sperm. Samples of cloacal fluid were examined under a microscope for motile sperm as evidence of recent copulation in females or attainment of breeding condition in males. Before release, the copperhead was marked with quick-drying enamel paint of a bright color, red, orange, yellow or blue, to facilitate recording of molt. Permanent marks were made to render the individual recognizable by clipping of subcaudal scales. I clipped these scales with sharp scissors by holding the tail firmly in place between the middle finger and hand, meanwhile maintaining the original grip on the neck between the thumb and forefinger (Plate 13, fig. 1). The subcaudals used for formulas were the second to the twentieth on the base of the tail. Each mark involved the excision of half a subcaudal on the left side of the tail and half of one on the right. The scale and underlying skin were removed, laying bare the muscle layer beneath. The excision involved two cuts with the scissors. Clipping was begun with the scissor points at right angles to the tail; the skin was slit at the base of the scale to be marked. Then the scissor blades were laid against the tail with the half-scale, now loosened on one edge between them, and it was removed with another stroke. In the copperhead, subcaudals except those on the distal part of the tail are normally undivided. The first entire subcaudal behind the anus was not clipped on either side, as in its absence the "number two" scale might have been mistaken for the first of the series. Three hundred and sixty-one combinations were possible with the remaining positions that were used. After these combinations had been exhausted, a new series was initiated duplicating the first except that a ventral body scale, the second anterior to the anal plate, on the left side "G 2 L"—gastrostege number 2 on the left side—was included in each formula. Subsequently other series, G2R, G4R, G5L and G6R were used in whole or in part. The G2R and G4R series were used exclusively for copperheads born in captivity or those first captured when they were near the size at birth. Any recaptured snakes bearing these marks were therefore at once recognized as individuals whose records extended back to the time of birth or near it.

Over periods of months the scale tissue always regenerated where the excisions were made, but the scar remained causing the area to differ slightly in color and surface texture from the intact scales nearby. Rarely the clipped scale was so well regenerated that only its narrowness, or an indentation on its posterior edge served for identification. The two or three excisions on an individual snake usually were not equally distinct at the time of recapture, and the factors affecting distinctness or obscurity after a period of years are not altogether clear. However if the anterior edge of the clipped scale remained, subsequent regeneration was much more complete.

Many copperheads were obtained by turning flat rocks, but these were only a small proportion of the total number taken. On the Reservation four comprised the maximum catch in one day by this method, but on other areas where the population was higher, ten or more have occasionally been secured in a few hours of rock-turning. The snakes are to be found most concentrated in the spring before they have left the rock ledges where they have hibernated, and they tend to be diurnal while nights are still cool. Nevertheless, a thorough search involving turning of every loose rock that was not too heavy, might disclose only one or two copperheads or none at all along a stretch of ledge where dozens were known to be present from the data obtained by live-trapping in autumn. Occasionally copperheads might be found under rocks at any time in their season of activity, but in summer hunting them in this way was less productive than in spring, because the snakes had dispersed from the hilltop ledges, and because at the high prevailing temperature and humidity the strenuous activity of turning heavy rocks produced relatively rapid fatigue.

A copperhead exposed by turning a rock usually lay motionless but alert for several seconds and then began moving slowly in search of shelter. Such snakes were usually caught without difficulty, but occasionally escaped when there were deep crevices readily available beneath or beside them.

Copperheads also were caught actively prowling on roads, usually at dusk or after dark. Temperature of the air and of the snake's body was usually recorded on these occasions. Some of the copperheads were obtained by chance in the course of routine driving, but many evening drives were taken expressly for the purpose of collecting them. Chances of finding the snakes were best when air temperature was higher than 75° F. and when the soil and vegetation were wet from recent rain, with humidity high. Upon approach of an automobile, a copperhead crossing a road usually retracted its head slightly and "froze" into immobility in a position from which it might strike an attacker or lunge for cover. Such individuals were more aggressive and irritable than those found under other circumstances; if touched or closely approached they would lash out wildly in self-defense, meanwhile thrashing and squirming in clumsy but animated attempts to reach shelter. However, such snakes found in open places usually could be held down with sticks and captured without difficulty.

Other types of data were obtained from the keeping of captives. An outdoor cage ten feet square, of quarter-inch wire in the shade of large elm trees near the Reservation headquarters was used to confine copperheads under conditions simulating their natural habitats. Natural vegetation grew in the pen but was kept trimmed to facilitate finding the snakes. Flat rocks and large boards provided shelter. A hibernation box was installed at a depth of three feet, with a removable insulation box between it and the surface permitting easy access to the snakes when they were dormant. A plastic tube with roughened inside surface (to permit traction as the snakes moved through it) provided a passageway from the hibernation box to the surface. General behavior, including feeding, breeding, activity, reactions to high and low temperature, and to sunshine, rain and other phases of the weather were observed in this cage. Another enclosure was constructed by installing a three-foot fence of quarter-inch wire extending in a semicircular arc 40 feet long, supported by metal stakes with each end against the outer wall of my residence. Much of the enclosed area could be seen from my bedroom window, which opened onto it, facilitating observations on natural activity. The pen contained natural vegetation and, as it had no top, birds, squirrels and other animals associated with copperheads in the wild moved freely in and out. Occasional opportunities to observe the mutual reactions of copperheads with such animals were afforded.

Still other copperheads were confined indoors, in cages in the laboratory or in my living-room. These provided types of information that rarely or never would have been obtained in the field such as frequency of shedding skin and fangs, rate of digestion, frequency of feeding, and various details of behavior. However, under the admittedly unnatural conditions of captivity indoors, normal behavior and physiology may have been altered somewhat.

DESCRIPTION

Lepidosis

The copperhead has lepidosis fairly typical of a generalized snake. Its cephalic scutes, for instance, correspond well in number and arrangement with those of most colubrids. In this respect the copperhead differs from crotalids of other genera, and even from some of the other species of *Agkistrodon*, in which there is a tendency for the scutes to be divided up into small, granular scales.

In the copperhead the cephalic scutes vary but little in their arrangement, either individually or in geographic populations. The shape and relative size of each scute is characteristic, and distinctive of the species. In the rostral plate, on the front of the snout, the width at the base exceeds the height but width at the top is slightly exceeded by its height. On top of the muzzle, bordering the rostral, are the paired internasals. They are subtriangular, expanded posteriorly, and wider than long. The nostrils are on the side of the muzzle approximately one-third of the distance from the tip of the snout to the eye. Each nostril is between a prenasal and a postnasal both of which contact the internasals, above and the first supralabial, below. The paired prefrontals, on top of the head behind the internasals, are wider than long, are rounded laterally, and are nearly as large as the frontal, supraoculars, and parietals, which are the largest cephalic scutes. On their posterior borders the prefrontals contact the frontal and supraoculars.

The loreal pit has an aperture about half again as large as that of the nostril. It is situated at the level of the lower edge of the eye, between the eye and nostril, but a little nearer the eye. The pit is bordered above by a supraloreal, an oval scale somewhat more pointed dorsally, and is bordered below by the infraloreal, a small, inclined, rectangular scale. The pit is bordered anteriorly by the second supralabial, and posteriorly by the lower preocular. The frontal is a pentagonally shield-shaped scale on the middle of the forehead, almost straight across the anterior end, with an angle of usually slightly less than 90° at the antero-lateral corner, often approximately 135° at the posterolateral corner, and slightly less than 90° at the posterior corner.

The paired parietals are half again as long as broad. They tend toward hexagonal or pentagonal shape but the posterior and postero-lateral margins are irregular and appear to be in process of breaking up into small scales. The anterior corner of each parietal forms an angle in the neighborhood of 90° (between the frontal and supraocular) and the two anterior sides are subequal. These two sides also approximate the length of contact of the two parietals with each other along the midline. The top of the head behind the parietals is covered with scales much smaller than those on any part of the body, arranged in irregular rows. A few of the more anterior are smooth, the rest are weakly keeled.

The supralabials are typically eight on each side. The first is low at the anterior end, and the length exceeds the maximum height. The second is higher than long and extends along the anterior margin of the facial pit to its upper edge. The third supralabial is much larger than the first or second, and subtriangular, low in front and high behind. The fourth is the largest, its anterior and posterior edges are nearly vertical; it is beneath the eye from which it is separated by two small suboculars. The fifth is similarly shaped but markedly smaller. The sixth is intermediate in size between the fourth and fifth, its rear edge inclined posteriorly. The seventh is higher than long and slanted posteriorly. The eighth is subtriangular, longer than high. There are two preoculars, horizontally divided, the upper approximately twice as large as the lower. The two suboculars are each about twice as long as high. There are three small postoculars (Plate 18, fig. 1).

There are several rows of temporals. The lower row is in contact with the supralabials. In the lower row, the first is relatively small and contacts the fourth and fifth supralabials. Temporals of the upper rows become progressively smaller and grade into the small scales on top of the head posteriorly.

Between the parietals and temporals, on top of the head, are four rows of moderately enlarged scales flattened and unkeeled and of somewhat irregular shape.

On the chin there is a mental rounded anteriorly, and forming an angle of about 110° posteriorly, followed by the first pair of infralabials, which are broadly in contact on the midline and are pointed posteriorly. Behind them there is a pair of genials, which are more than twice as long as wide, are in contact medially, and are bluntly pointed posteriorly. Behind the genials and between the infralabials and anterior ventrals are the gulars in approximately six rows, but the rows are somewhat irregular. The gulars are mostly rectangular or vaguely hexagonal, from two to three times as long as broad. There are ten pairs of infralabials; those of the second pair are only about half the size of the third pair and a quarter the size of the fourth pair. Beyond the fourth pair size becomes progressively smaller. The last two are elongate, others are rhomboidal, slightly higher than long.

On the neck the dorsal scales are markedly smaller than those elsewhere on the body (about one-fourth the dimensions of a typical body scale) and they resemble those on the posterior part of the head. There are slight irregularities in the scale rows of the neck and of the posterior part of the head, resulting from the merging in this region of rows having scales of different sizes and shapes—the gulars, the scales above the temporals, and the body scales. The body scales overlap slightly except when the skin is stretched. In the region of the throat, neck, and forebody the skin is especially loose and elastic. When the snake is swallowing prey, for instance, the skin may be stretched to the extent that two neighboring scales are separated by areas of skin much greater than their combined widths (Fig. 3). Farther posteriorly, especially past mid-body, the skin is much less extensible. The body scales are keeled (except those of the anterior part of the first row). A typical scale is approximately twice as long as broad tending toward an oval shape with the posterior end the more pointed; scales are often faintly hexagonal. The dorsal scales near the midline are the narrowest; those farther down on the sides become progressively wider. Farther posteriorly on the body, and especially on the tail, the scales become smaller, and relatively wider, tending to a rhomboidal shape.

There are 23 scale rows on the body for most of its length. In the neck region, however, counts of 25 rows or even more, can be obtained. The fifth row on each side drops out at a point averaging 11 per cent of the distance from snout toward the vent (in the neighborhood of the 17th ventral) leaving a total of 23 for most of the length. At a point averaging approximately 70 per cent of the distance from snout to vent (in the neighborhood of the 102nd ventral) the fifth remaining row (originally sixth) drops out on each side leaving a total of 21, and at a point approximately 87 per cent of the distance to vent the fifth of the remaining rows (originally seventh) drops out, leaving only 19 rows on approximately the posterior 13 per cent of the body.

On the tail the remaining rows drop out in rapid succession. At the middle of the tail there are only ten rows and just ahead of the tail spine there are only three. The tail ends in a blunt spine, which is inclined downward slightly at the tip (Fig. 4). Cope stated (1900:1132) that the spine consisted of three scales, one ventral and two dorsal, ensheathing the last caudal vertebrae, an elongate, pointed splint. However, in the specimens that I have examined, the caudal spine consisted of a single scale, with a seamlike ridge along the mid-dorsal line but none ventrally, with another enlarged, platelike scale at the base of the spine on the dorsal surface of the tail.

According to Gloyd and Conant (1943:168), ventrals averaged 148 in 820 specimens of *A. c. mokeson*, with no difference in numbers between the sexes. In the same series, subcaudals averaged 46 in males and 44 in females. To judge from the relatively few counts made in the course of my study of the local population the average numbers of scales does not differ from the numbers recorded by Gloyd and Conant (*loc. cit.*).

Color and Pattern

The color is predominantly brown, but with different shades, in a boldly contrasting pattern, from pale grayish brown, tan, or fulvous at one extreme to a deep chestnut, nearly black at the other. The range of shades is great when one takes into account individual variation, age variation (the young are paler, with more vivid pattern and lack reddish suffusion), variation caused by the cycle of molt (colors become darker and duller as the time of shedding approaches), and sexual difference (the adult males are darker, with more reddish suffusion, as compared with most females).

The head is reddish brown dorsally, having a color vaguely reminiscent of that of an old copper coin, hence the most common vernacular name of the species. In each parietal plate near its center but slightly displaced toward the midline of the head, there is a spot of dark chestnut, narrowly rimmed by fulvous. These parietal spots are conspicuous although they are usually less than one millimeter long, even in the largest specimens. The brownish hue of the head deepens in the temporal region, and is separated by a sharply defined line from the much paler cream-colored area of the supralabials. The line of separation passes from the eye posteriorly through the middle of the first temporal, through the lower part of the second temporal, and along the upper edges of the last two supralabials. The infralabials also are cream-colored, paler than any other part of the snake, but their ventral (medial) portions are darkened, with a sharp line of demarcation between the pale and dark portions, running continuously from the second to the last. This line on the infralabials joins or almost joins the posterior end of the line across the temporal region, the two forming a narrow loop around the corner of the mouth. The anterior part of the head is more grayish (less reddish) than the posterior part, and there are no markings on the rostral region.

Over the entire body the scales are finely stippled with black dots. Typically there are from 20 to 40 per scale but the number cannot be counted accurately because some are in contact or partly fused with others. On the body there is a series of dark brown cross bands on the lighter brown ground color. The cross bands have been described as hourglass-shaped or dumbbell-shaped; they are constricted in the midline and widened laterally. At its medial constriction a band of symmetrical shape is usually of a width equal to the combined lengths of three or four dorsal scales. On the side, at its widest extent, the band is usually eight to ten scales long—wider than the interspace which is usually three to six scales long at this level on the side. Many of the bands are not bilaterally symmetrical, but the half on one side of the midline is displaced either anteriorly or posteriorly with respect to its partner on the opposite side, with the result that the left and right halves have only a narrow connecting zone or are completely separated. Individuals having all their cross bands intact are in the minority. A band may be represented by only the left or right half, with no counterpart on the opposite side of the midline. Or on the left or right the band may be represented by a mere spot on the lower part of the side, not extending to the midline. The number of intact bands varied from seven to 16 in the copperheads examined, but 12 was the most frequent number. Livezey (1949:93) figured an abnormally patterned copperhead from Texas in which only three of the 14 bands on the body were intact. In individuals having the number of complete bands fewer, the number of half-bands, or blotches is correspondingly greater, and the proportion of the body covered by the chestnut markings seems to be remarkably constant (Figs. 5 and 6). Secondary sexual differences in the number and disposition of markings were not clearly indicated by the trend of the data. The trends for the left and right side showed no consistent differences either. The transverse dark markings of the body are continued onto the tail, but there they are not constricted middorsally, and the paler interspaces become progressively smaller until they are represented by only thin lines on the posterior part of the tail. On the average, there are approximately eight dark marks on the tail.

The chin and throat are pale, cream-colored (except for the dark area on the infralabials, already mentioned). The ventral surface of the body has large, irregular, black marks that occupy the greater part of its surface. These markings are mainly on the ventral plates, but they invade or include some scales of the first row adjacent to the ventrals. The markings have sharply defined lateral edges, but elsewhere their edges are so diffuse and ill-defined that no definite count can be made of the number present; rather the general effect is of marbling or heavy but uneven stippling over most of the ventral surface. The larger ventral markings are rounded and usually cover parts of three or four adjacent ventrals. Ordinarily there is one on each side beneath each dorsal cross band and one beneath each of the paler areas alternating with the cross bands. The markings are better defined on the anterior part of the ventrum than they are posteriorly; on the tail they are especially vague.

The lining of the mouth is flesh-colored. The tongue is carmine, paling to white on the tips. The iris of the eye is pale gold with fine reticulations of dark pigment. As in all other pit vipers the pupil is vertically elliptical.

Size

Copperheads captured on the Reservation ranged from 209 mm. to 936 mm. in snout-vent length (9.8 inches to 42.0 inches in over-all length). Many smaller than 209 mm. were born in captivity, but probably most or all of these young were stunted by the unfavorable effects of confinement on the gravid females. In a sample of 1,678 records from the Reservation, 1949 to 1959, the average over-all length was 22.4 inches. Figure 7 shows the relative numbers in each size class, of each sex. It is evident that maximum size is larger by one-fourth in males than in females. Most typical adult sizes are 28.5 inches for males and 26 inches for females, in over-all length.

Almost nothing is known concerning geographic variation in size over the copperhead's extensive range, but there is some indication that western populations do not grow so large as those in the eastern states. The largest copperhead ever recorded in the literature was 53 inches long, and was captured at

White Plains, New York, in the northeastern part of the range (Ditmars, 1935:22). Others nearly as large have been recorded from this same general area. It is unlikely that this size is even approached by the largest individuals in Kansas. Wright and Wright (1957:904) recorded that a Mr. C. L. Love took a 52-inch specimen at Apopka in central Florida, but some mistake must be involved here as the locality is well outside the authenticated range of the copperhead. The same authors stated that adult size was 16 to 36 inches in the western *A. c. laticinctus.* Oliver (1958:40) stated that the Trans-Pecos

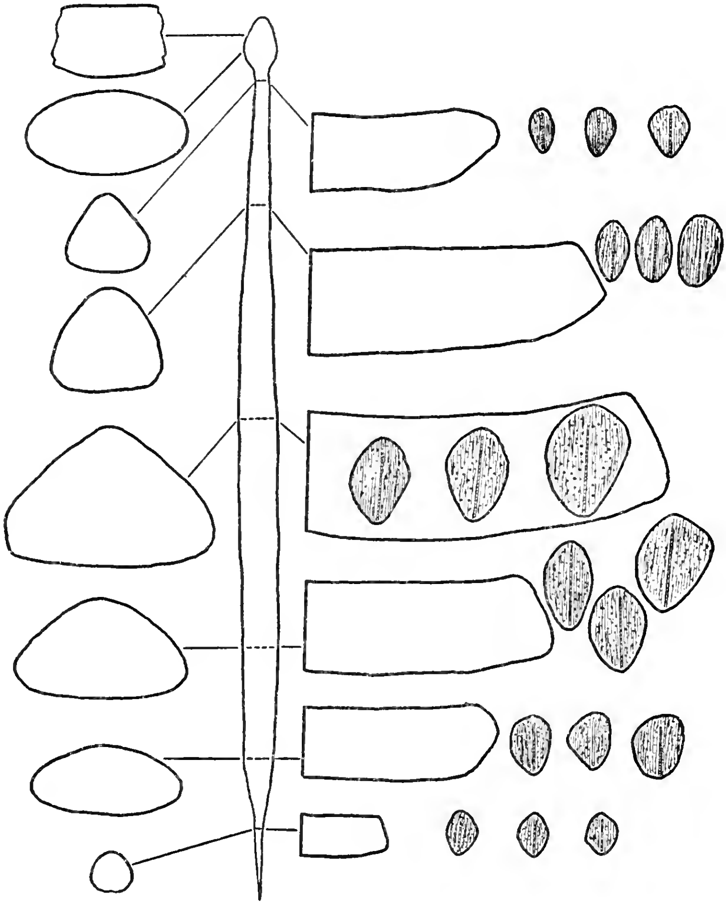

FIG. 2. Bodily proportions, and relative sizes of scales in a copperhead. Column on left shows two cross-sections of the head, five of the body and one of the tail. On the right are shown ventral scutes (right halves only), and dorsal scales (shaded) in series of three, representing one from near mid-dorsal line (farthest left), one from halfway down the side (middle), and one from low on side, adjacent to ventral scute (right). Snake shown approximately × 1/6, cross-section × 5/6, scales × 3.

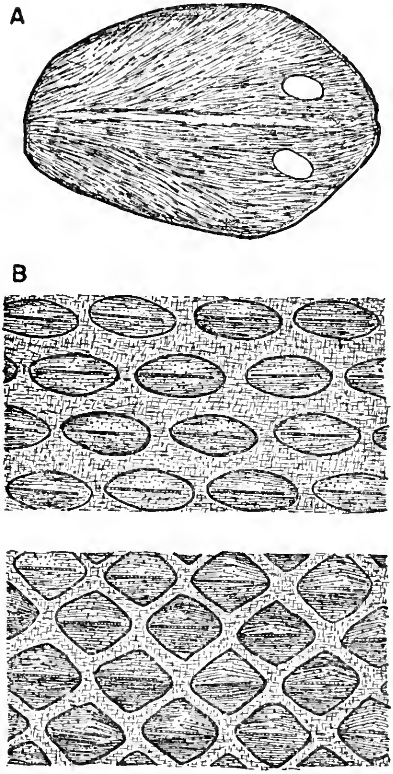

FIG. 3. A. Scale of a copperhead, × 15, showing keel and apical scale pits. The anterior end of the scale is on the left. B. Skin of a 27-inch copperhead, moderately stretched, on forebody (above) and on rear of body (below) × 4. Skin is much more extensible on anterior half of body, permitting ingestion of bulky prey.

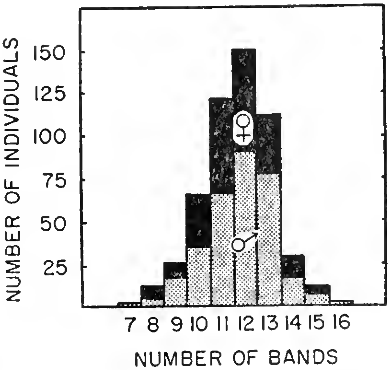

FIG. 5. Number of intact crossbands on body in copperheads from area shown in Fig. 1. Bands that are broken at the mid-dorsal line or those that are represented on only one side of the body are excluded. Trends are similar for both sexes.

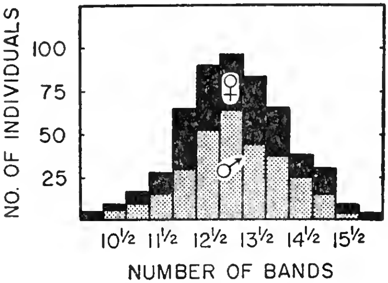

FIG. 6. Number of cross bands on body in same group of copperheads represented in Fig. 5, but including bands that are broken in the middle and those that are represented on only one side of the body.

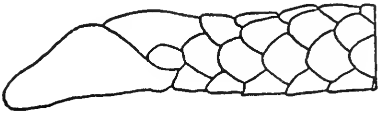

FIG. 4. Diagram of tip of tail of a 30-inch copperhead (× 7).

copperhead, *A. c. pictigaster* seems to attain a maximum length of only two feet. However, only a few typical specimens of this subspecies are known, and all of them may be far short of maximum size.

Bodily Proportions

The form is that of a typical crotalid. The head is flattened and subtriangular, much widened in the posterior temporal region, and abruptly tapering anteriorly to the muzzle, which is somewhat rounded. From the eye to the snout the top of the head is in a plane at right angles to its side, and a sharp edge, the *canthus rostralis,* is formed. The posterior part of the head is laterally elliptical in cross-section. The neck is constricted. The body is moderately robust, subtriangular in cross-section, and increasingly flattened posteriorly. The tail is round in cross-section, tapers abruptly, and is relatively short—usually from one-sixth to one-seventh of the snout-vent length, depending on the age and size of the individual. For 23 specimens, of both sexes and various sizes, that were measured when freshly killed and relaxed, the following proportions were obtained, expressed as ratios of snout-vent length:

Length of head, 5.55 ± .11 per cent
Width of head, 4.14 ± .08 per cent
Circumference of neck, 6.81 ± .13 per cent
Circumference at mid-body, 10.41 ± .16 per cent
Circumference of tail base, 6.59 ± .12 per cent

None of these characters showed any significant differences between the sexes. However, relative head-length, and head-width was found to be greater in the smaller snakes, progressively decreasing as greater over-all

TABLE 1. VARIATION IN RELATIVE TAIL-LENGTH ACCORDING TO SIZE AND SEX IN A POPULATION OF COPPERHEADS

SIZE GROUP; SNOUT-VENT LENGTH IN MM.	Males		Females	
	Number in sample	Ratio of tail to snout-vent length; mean, standard error, standard deviation	Number in sample	Ratio of tail to snout-vent length; mean, standard error, standard deviation
200–250....	68	17.55±.143 1.18	26	17.20±.055 .282
251–300....	39	17.35±.177 1.11	15	16.40±.0384 .149
301–350....	33	16.40±.131 1.31	29	16.10±.179 .78
351–400....	40	16.52±.108 .685	39	15.75±.160 .91
401–450....	53	16.49±.13 .95	27	15.1 ±.127 .66
451–500....	62	16.20±.161 1.27	27	15.2 ±.094 .586
501–550....	66	16.05±.103 .84	67	14.8 ±.086 .70
551–600....	72	15.90±.087 .74	97	14.65±.075 .74
601–650....	75	15.89±.076 .66	64	14.27±.084 .674
651–700....	77	15.55±.087 .76	36	13.85±.099 .593
701–750....	39	14.80±.139 .87		
751–800....	30	14.46±.173 .96		
801–850....	18	13.94±.100 .43		
851–900....	15	13.43±.334 .75		

length is attained (Figs. 8 and 9). Klauber (1956:152) has discussed at length similar changes of proportions in the rattlesnakes.

Like other kinds of snakes, the copperhead exhibits sexual dimorphism in the relative length and proportions of the tail, and in its ratio to body-length. However, in the copperhead the sexual dimorphism is relatively slight and tends to be obscured by ontogenetic changes. Table 1 shows the changing ratios of tail-length to snout-vent-length in males and females, grouped in 50 mm. intervals.

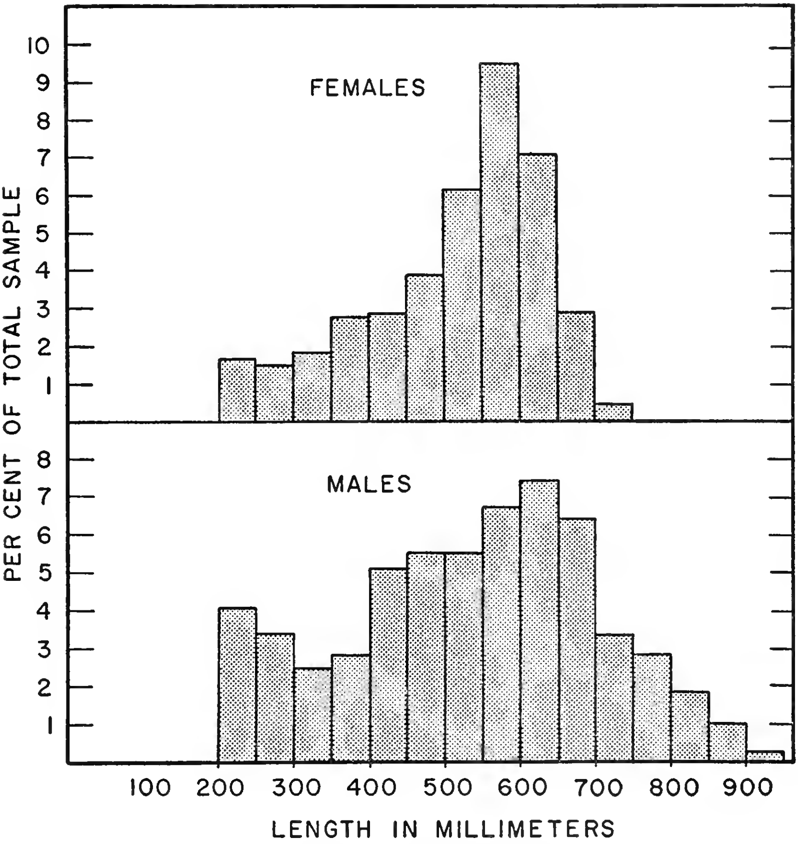

FIG. 7. Sexes and size-groups (snout-vent length in 50-millimeter intervals) in a sample of 1,678 copperheads from the area shown in Fig. 1. Males are more numerous and attain considerably larger size. In females, growth slows more abruptly after attainment of sexual maturity and adults are concentrated in the size-group of 550 to 600 millimeters.

In newborn young of both sexes tails are generally between 17 and 18 per cent of the snout-vent length. Sexual dimorphism is not readily discernible in individuals, but the tails of the males average longer and the difference is statistically significant. As the young snakes grow, the difference in proportions increases gradually. In young adults, males and females can be easily distinguished, and the sex is even more readily discernible in old adults. In both sexes the tail becomes relatively shorter as size increases. The trend is more pronounced in the females. However, growth continues longer in the males, and as a result, large adult males (900 mm. snout-vent) and large adult females (700 mm. snout-vent) resemble each other in ratio of tail to snout-vent length.

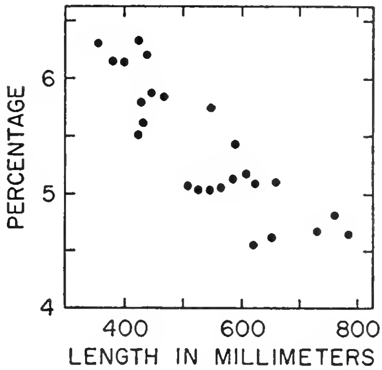

FIG. 8

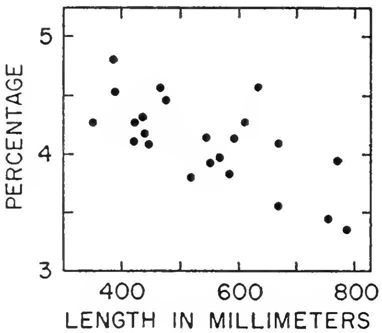

FIG. 9

FIG. 8. Head-length expressed as a percentage of snout-vent length in copperheads of different sizes. The head grows less rapidly than the body, and consequently is relatively small in the largest and oldest snakes.

FIG. 9. Head-width expressed as a percentage of snout-vent length in copperheads of different sizes. The trend parallels that shown in Fig. 8.

Dentition

Compared with most other snakes the pit vipers, including the copperhead, have their teeth reduced in number, enlarged, and specialized. The dentigerous bones are, in the upper jaw, the premaxillary (bearing only the fetal egg-tooth), the maxillary bearing the poison fang, the palatine, and the pterygoid; and in the lower jaw, the dentary. The teeth are all thorn-shaped—elongate and conical, widened at their bases and more or less curved, with the points directed posteriorly and medially. Movements of the jaws tend to pull any object grasped in the mouth farther back into the throat. The dentary bone bears 15 or 16 teeth; the first one, at its anterior end, is slightly depressed. This first tooth is directed anteriorly at its base but is curved and the point is directed almost straight upward. The second dentary tooth is slightly larger than the first and is situated higher on the bone; this second tooth is slightly recurved and stands out as the largest and most conspicuous tooth of the dentary series. The other teeth are of progressively decreasing size posteriorly, and are increasingly recurved. The last dentary tooth is less than half the size of the first two.

The palatine bears five teeth, all relatively small and strongly recurved.

The pterygoid bears 13 to 17 teeth, all strongly curved, and becoming smaller toward the posterior end of the series.

The numbers of teeth mentioned above as characteristic for each dentigerous bone refer to the number of sockets, but at any one time some are empty, as teeth are shed frequently. The shed teeth pass through the digestive tract little altered, and a fecal mass that is examined microscopically usually is found to contain many of them.

The maxillary is remarkably modified from the typical ophidian form of an elongate arcuate bone in the anterior supralabial region. Instead it has in the course of evolution become shortened chiefly by loss of its posterior part, but extended in a vertical plane, and it is considerably deeper than long. Its lateral face is excavated to accommodate the sensory facial pit. The maxillary articulates posteriorly with the prefrontal, palatine and ectopterygoid. Because of its shortened form, the maxillary can rotate through almost 90°, permitting its single greatly enlarged tooth, the solidly attached poison fang, to be either erected or folded against the roof of the mouth. Each maxillary bone bears twin sockets side by side, but, in the frequent replacement of fangs that occurs, there is alternation from one socket to the other. Both sockets bear fangs simultaneously only in a relatively brief interval when one fang is about to be shed and the other has just become anchored to the bone.

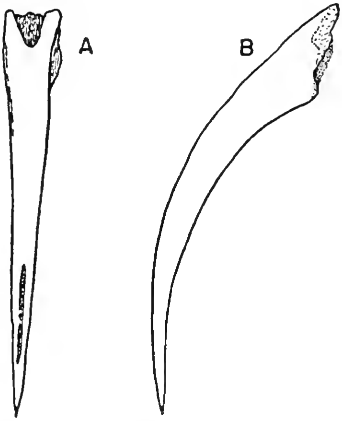

FIG. 10. Right fang of a copperhead from (A) anterior view and from (B) lateral view, × 9.

The poison fang is similar in general appearance to the other teeth, but much enlarged. In its evolution it has been converted from a simple conical structure to a tube, functioning like a hypodermic needle in the injection of venom. Presumably in remote ancestors of the pit vipers the fang first developed a groove on its anterior surface, as a channel down which the venom might flow into the wound inflicted by the tooth. Eventually the groove became deeper, and its sides extended medially to contact each other, enclosing the venom canal as a tube. Even in the modern pit vipers the venom canal is not entirely enclosed for the full length of the fang, but the lumen appears as an elongate slit on the anterior surface of the fang's distal one-third. The venom thus is injected to a depth somewhat less than the length of the fang. The tip of the fang is solid. Venom enters the fang through a notch near the base on its anterior face, enclosed deep in the sheath.

During its short functional life, the fang is rigidly attached to the bone, in its socket. After a new fang has assumed its position in the alternate socket, the first fang becomes weakened at its base, and breaks off by means of an irregular fracture when subjected to stress. Even after fracture occurs the fang may be retained for a day or more inside its fleshy sheath, loosely attached to the gum tissues or incompletely separated from its pedicel. Eventually it becomes detached and is swallowed along with the food. The pedicel is then resorbed into the socket.

At any one time a copperhead has several replacement fangs in various stages of development in the gum behind the socket bearing the functional fang. Each socket has its own series of replacement fangs. The tip of the fang is the part formed first, and calcification gradually proceeds toward the base. The base of the fang is formed within its socket, and until calcification is completed in this region the fang is loose.

In 1956, 1957, 1958 and 1959 I examined the fangs in 745 of the live copperheads collected on the Reservation. In 248 there was an accessory fang on either left or right side, and in 23 there was an accessory fang on both sides. Thus 294 fangs, or 19.7 per cent of the 1490 fangs in this entire group of snakes, were being replaced. These figures suggest that for about one-fifth of the time on the average, each fang is in process of replacement. A small adult female copperhead was kept active at room temperature through the winter of 1959-1960 and examined at irregular intervals of two or three days. On December 15 the right fang was being replaced and by December 19 the process was completed. On December 23 an accessory left fang was in evidence and on December 28 it was solidly attached in its socket beside the old left fang. On December 31 the old left fang was loose in its sheath and was removed with forceps. On January 15 an accessory right fang was again in evidence but was still loose and in a position behind the old fang. On January 17 there was little discernible change, but on January 20 new and old right fangs were side by side in their sockets. On January 24 the old right fang had been shed. On January 27 an accessory left fang was again in evidence still loose and behind the old fang. On January 30 the new fang was still slightly loose and behind the old fang. On February 2 one left fang, presumably the older, was loose and in a position behind the functional fang.

In this snake, for the seven-weeks observation period, left and right sides alternated in replacement of the fang, with approximately a 33-day cycle on each side, and with known replacement periods extending over five, six and eight days, during which both new fang and old fang were in evidence on the same side. The new and old fangs were simultaneously functional during only a small part of the replacement period. Although the snake upon which these observations were based, was kept at slightly lower temperatures than those prevailing under natural conditions during most of the copperhead's season of activity, it seems reasonable to conclude that the normal cycle of replacement for each fang is slightly more than a month with a replacement period of approximately a week. Klauber (1956:726) estimated the normal functional lifetime of a fang to be six to ten weeks in an adult rattlesnake.

Length of fangs is variable. In 52 shed fangs, measured from fractured edge of base to tip, in a straight line, the average was .873 per cent of the snout-vent length. For 21 copperheads in the size range 500 to 600 mm. (small adults) the fang length averaged .88 ± .0144 per cent of the snout-vent length. At birth the young have relatively large heads and the fangs are longer in proportion to the snout-vent length than are the fangs of larger and older individuals. Although my samples were too small to show how these proportions change, the following figures are suggestive of the trend.

TABLE 2. CORRELATION OF RELATIVE FANG-LENGTH WITH SNOUT-VENT LENGTH

SNOUT-VENT LENGTH (millimeters)	Number in sample	Average ratio of fang-length to snout-vent length (per cent)
300–399	5	.95
400–499	10	.89
500–599	21	.88
600–699	9	.83
700–799	4	.86
800–899	2	.78
900–999	1	.70

Klauber (*op. cit.*:732-737) has discussed in detail similar length relationships of the fangs in rattlesnakes. He showed that in the course of ontogeny relative fang-length changed not only in proportion to over-all length but in proportion to head-length. Fang-length to head-length ratio reaches its maximum in adolescent rattlesnakes. Shape of the fang also changes in ontogeny; in young the curvature is fairly uniform for the fang's entire length, but in adults the distal part of the fang is slightly recurved. Parallel changes occur in the ontogeny of the copperhead.

Klauber presented figures to show the relative fang-lengths in all species of rattlesnakes. Fangs were measured from the tip of the notch of the basal lumen, excluding the more proximal part of the fang on the grounds that the plane of fracture across the pedicel was variable. Also, fang-length was computed as a percentage of over-all length (including the tail) rather than of snout-vent length. In 17 copperhead fangs that I measured according to Klauber's method, the lengths were, on the average, .63 per cent of the snakes' over-all lengths—much shorter than in any rattlesnakes. By way of contrast various species of rattlesnakes listed by Klauber (*op. cit.*:736) had fangs in the following length ranges expressed as a percentage of over-all length (disregarding certain subspecies that differed from typical representatives of their species).

.80 per cent to .89: *Crotalus adamanteus, molossus, polystictus,* and *stejnegeri*
.90 per cent to .99: *C. exsul* and *ruber*
1.00 per cent to 1.09: *C. atrox, unicolor, pusillus, durissus* and *horridus*
1.10 per cent to 1.19: *C. willardi, triseriatus, tortugensis, viridis* and *cerastes*
1.20 per cent to 1.29: *C. basiliscus* and *scutulatus*
1.30 per cent to 1.39: *Sistrurus catenatus* and *C. enyo*
1.40 per cent to 1.49: *Sistrurus miliarius* and *C. lepidus*
1.50 per cent to 1.59: *C. mitchelli* and *pricei*
1.60 per cent to 1.69: *C. tigris*
1.90 per cent to 1.99: *C. transversus*
2.00 per cent to 2.07: *C. intermedius*

Hemipenis

As in other snakes, the paired copulatory organs are lodged in the base of the tail. There are distinctive differences between the hemipenes of different kinds of snakes that are useful in defining species and genera. Cope (1900, pl. 31, fig. 4) has illustrated the hemipenis of the copperhead, but his figure bears little resemblance to the organ, as seen when everted. Cope's drawings of hemipenes seem to have been based on observations of those invaginated in the normal position of repose in the tail in preserved material (*fide* Herndon G. Dowling), but were drawn as Cope imagined they would appear when everted.

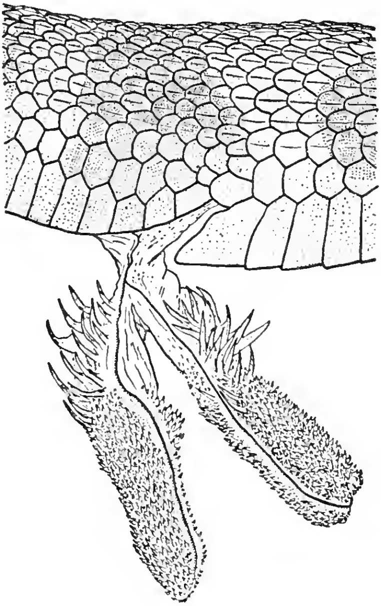

FIG. 11. Right hemipenis of a copperhead from lateral view, everted but not fully distended. The organ is deeply bifurcate, with large spines near the base and numerous spinules on the distal part of each lobe (× 3).

Klauber (1956:661-668) has well described the hemipenes of the many species of rattlesnakes and has illustrated several. In most respects these organs resemble that of the copperhead, but differ in various details. In the copperhead (Fig. 11) the hemipenis is deeply bifurcate (for about three-fourths of the total length). The lobes tend to be cylindrical and are only slightly tapered distally, but are enlarged at their bases, and are approximately three times as long as broad. There are approximately 35 large spines on the basal thirds of the two lobes. Most of these spines are straight but some are slightly hooked. The distal two-thirds of each lobe is covered with small flattened papillae, each ending in a spine. There are probably more than a thousand of these papillae on each hemipenis but they are not arranged in regular rows. The transition from the spiny basal portion of each hemipenis to the papillose distal portion is abrupt. There are no mesial spines in the crotch. The sulcus spermaticus is forked near its base.

RELATIONSHIPS

The copperhead is among the more primitive representatives of the Crotalidae (pit vipers), which is one of the most specialized families of snakes. In lacking a rattle, in having enlarged head shields typical of the more generalized colubrid snakes, in having only those subcaudals on the proximal part of the tail undivided, and in having the poison fangs relatively short, the copperhead is less specialized than other crotalid genera, the rattlesnakes, (*Crotalus* and *Sistrurus*), fer-de-lance and its relatives (*Bothrops*), oriental pit vipers (*Trimeresurus*), or bushmaster (*Lachesis*).

The genus *Agkistrodon* includes perhaps a dozen species (see Smith, 1943:494), but some of these are wide ranging and highly variable in their characters, and authorities differ as to the number of full species that should be recognized. Dr. Howard K. Gloyd is engaged in a taxonomic revision of the genus.

Some characters of the genus are: pupil of eye vertical; head covered with symmetrical shields (or having the internasals and prefrontals broken up into small scales); facial pit between the preoculars and loreal; scales usually keeled (smooth in *A. rhodostoma*); anal plate single; subcaudals either undivided or divided in pairs—usually both conditions occur in the same individual on different parts of the tail; anterior genials large, posterior genials small or ill-defined.

Though having these characters in common the species differ strikingly in size, color, pattern, numbers of scale rows, arrangement of cephalic shields, and also in habits and habitats. Obviously the genus is relatively old as compared with most other vertebrate genera, and its species are well differentiated.

The cottonmouth (*A. piscivorus*) shares much of the copperhead's range, and perhaps is its closest relative. The basic pattern is similar in the two species, and various behavioral traits are shared by both. The young are more nearly alike than the adults, and might easily be mistaken for each other. But in size, habits and habitats, and in various features of external morphology the two species are sharply differentiated. The cottonmouth is much larger; individuals six feet long are on record. It is partly aquatic and is usually found in or near streams, lakes or sloughs. It preys mostly on amphibious or aquatic vertebrates. The cantil (*A. bilineatus*) resembles the cottonmouth in habits but is perhaps less aquatic as on occasion it has been found far from water. The cantil's range is complementary to that of the cottonmouth, and is in Mexico, chiefly in the coastal lowlands. Its color pattern is readily derivable from that of the cottonmouth but is less like that of the copperhead.

Of the Old World species, (Pope, 1935:386-403 and 1955:222-223; Smith, *op. cit.;* Schmidt and Inger, 1957:264-267) none seems to be closely related to the copperhead. Perhaps *A. acutus* of southern China resembles it most. The Old World species are confined to forests of southern (mainly southeastern) Asia except for *A. halys* which ranges from Japan westward through both forests and steppes to the Caspian Sea. Compared with the North American species the Asiatic species form a much less compact group and differ greatly among themselves in size, scalation and habits. *A. acutus* attains a length of five feet, but 34 inches is more typical for other species (*rhodostoma, himalayanus*), and the smallest species *strauchi* is only 20 inches long. Most of the species are viviparous but *acutus* and *rhodostoma* are oviparous. Scale rows number 21 in most of the species, but only 17 in *hypnale* and *nepa*. The scales are keeled in most species, but are only faintly keeled in *hypnale* and *nepa* and are smooth in *rhodostoma*. In *acutus* and to a lesser extent in *hypnale* and *nepa* the snout is drawn out into a pointed dermal appendage covered with small, irregular scales. *A. hypnale* is further peculiar in lacking hemipenial spines. *A. rhodostoma* and *hypnale* have been described as vicious while *himalayanus* and *halys* are inoffensive and will not bite even when handled. *A. strauchi, monticola* and *himalayanus* are montane species of which the latter has been recorded at an extreme altitude of 16,000 feet. In all the species the colors run to grays and browns, with a series of blotches or rhomboidal or triangular or wavy markings on each side which seem to be homologous with the bands of the copperhead.

The wide geographic hiatus between the Old World species and those of the New World calls for comment. Schmidt (1946:150) mentioned *Agkistrodon,* along with various other reptilian genera (*Natrix, Liopeltis, Elaphe, Leiolopisma* [= *Lygosoma*], *Eumeces, Ophisaurus, Alligator, Clemmys* and *Emys*), which have representatives in both Eastern North America and Eastern Asia and which seem to be remnants of a late Cretaceous or early Tertiary Holarctic fauna, which was forced southward and partly destroyed as northern climates gradually became more severe in a trend that culminated in the Pleistocene glaciations. The genera mentioned are ancient and conservative and some of them are known to have changed but little throughout the Tertiary period when more progressive groups of terrestrial vertebrates were undergoing rapid evolution.

The fossil record is too meager and too recent to shed any light on the evolution or relationships of the pit vipers. All known fossil pit vipers from North America are of Pleistocene age with the exception of those from Driftwood Creek, Hitchcock County, Nebraska, which have been tentatively assigned to the lower Pliocene (Brattstrom, 1954:35). The fauna from these deposits includes the copperhead and the prairie rattlesnake (*Crotalus viridis*). The copperhead material according to Brattstrom (*loc. cit.*) consists of 31 vertebrae, which do not differ from those of Recent specimens. It is noteworthy that the locality is 160 miles farther west than the northern copperhead's present western range limits, and is also slightly farther north than the copperhead's range extends, except in the region of the Atlantic Coast. Evidence is provided that in earlier times the copperhead's range was perhaps more extensive and in any case extended well to the north and west of its present limits. Almost certainly, the deciduous forest habitat likewise extended westward into this area which is now high plains. It is noteworthy also that fossils of copperheads and prairie rattlesnakes should be associated. At present these two species of crotalid snakes, whose combined ranges include most of the United States, overlap only slightly in Kansas, Oklahoma and Texas; their ranges are mainly complementary since their habitat preferences are entirely different. Presumably in the early Pliocene their habitats were less sharply segregated; also possibly the snakes themselves may have been less differentiated in their habitat preferences. Chaney and Elias (1936:27) found that in the lower Pliocene the grasslands of the Great Plains were much less extensive than they are at present. Rainfall was estimated to be 15 inches higher than it is at present and supported a mesic deciduous forest some 180 miles farther west than the present limits of such forests. However, the copperhead and all but one of its congeners are committed to a forest habitat, as are, predominantly, all the other genera of reptiles shared by North America and Eurasia. It seems that these genera, which Schmidt (1946:144) has termed "Old Northern," date back to a time in the early Tertiary when the North Pacific was bridged by land areas that were well forested. An early Tertiary flora dominated by deciduous forest is known from Alaska (Hollick, 1936:11), and a similar Miocene deciduous forest is known from the region of the Columbian Plateau (Axelrod, 1950: 230). Chaney (1947:147) described an Arcto-Tertiary deciduous forest widely distributed in the Northern Hemisphere, with striking uniformity throughout, as late as the Miocene. From the Miocene onward regional diversity developed, especially for the less cold-tolerant elements, for which climatic barriers developed. These Tertiary forests had many elements in common with the Recent Deciduous Forest Biome of southeastern North America. Probably this Recent deciduous forest was derived directly from the more northern Tertiary forests by gradual alteration, chiefly impoverishment, and retreat or shrinkage southeastward as a result of the trend toward cooler and drier climates.

HABITAT

Usually associated with forests, the copperhead inhabits several types of deciduous forest climaxes and many of their seral phases. The species displays considerable versatility in adapting to varied habitats from swamp to desert and from sea level to high mountains over its wide range. Although geographic populations differ somewhat ecologically, all have in common certain basic requirements. There is definite preference for ground that is shaded by a leaf canopy and blanketed with leaf litter from deciduous trees. Preferably this substrate should be wet or at least damp during the time that the snakes are active. However, copperheads may wander into brush, grassland, or weedy fields, and may prowl on a dry substrate.

The following briefly quoted statements from the literature and from field notes show the range of habitat preferences throughout the geographic range.

". . . chooses dark and shady places for its residence in general, though at times it is found in meadows of high grass." (Holbrook, 1838:71.)

Northeastern states: ". . . rocky places, usually in the vicinity of moderately thick timber, marshy glades, or hollows." (Ditmars, 1907:422.)

". . . rocky ridges and ledges, usually in the vicinity of fairly thick timber. . . . During the height of the summer they often descend to the meadows and valleys." (Babcock, 1929:26.) "Ledgy, wooded hills with a base of wild, damp meadows, are the favorite prowling grounds of this snake, as it searches for small rodents, birds and frogs. During the summer it is often seen along old stone walls which might offer shelter and a congregating place for rodents." (Ditmars, 1935:24.)

Connecticut: ". . . meadows and low-lying ground. . . . finds concealment in the rocky parts of the country, and still remains in the trap ridges of the Connecticut Valley. . . ." (Cope, 1900:1138.) ". . . ledgy hills, with base of wild, damp meadows or nearby heavy forest. During the summer it is often seen along old stone walls. . . ." (Lamson, 1935:26.) ". . . loose rock ledge. Cedars, pines, laurel and blueberry bushes are the predominant vegetation." (Finneran, 1948:124.)

New York: ". . . generally found in meadows, pastures, and the edge of woods." (Rafinesque, 1819:86.)

Pennsylvania: (Union County) ". . . mountains . . . [and] lowlands along streams." (Pawling, 1939:169.) (Venango County) ". . . top of hills in August (many are killed cutting wheat) . . . back into the valley in September. In July there seem to be more along the weedy shore of the river than on the rocky hillside." (Swanson, 1952:176.)

Maryland: (Harford County) ". . . rocky mountain sides, ledges, and accumulations of talus. . . . During the summer . . . about stone walls, the edges of fields, old foundations, sawdust piles, and in wooded areas." (McCauley, 1945:131.)

Virginia: (Giles County) ". . . common in valleys throughout the county." (Hutchison, 1956:85.) (Stafford County) ". . . very abundant . . . found on rocky hillsides bordering Aquia Creek and in the slab piles of abandoned saw-mill sites in the woods. A number were found, however, along road sides and in open fields." (Lynn, 1936:170.) (Princess Anne County) ". . . dense deciduous woods. . . ." (Werler and McCallion, 1951:251.)

North Carolina: ". . . old building sites, rock piles such as old stone fences and brier thickets in former clearings. It has been taken several times from under the fallen bark about the bases of dead chestnut trees. . . . not usually . . . above 2500 feet." (King, 1939:577.) ". . . edge of a cypress swamp adjoining open fields." (Robertson and Tyson, 1950:143.) (Dismal Swamp region) On pine needles in trail, beside drainage ditch in woods of cypress and pine, with ferns and canebrake. Under log at edge of cornfield near wet woods and large water-filled ditch. Trail overgrown with honeysuckle, behind an abandoned shack. On dirt road a few hundred feet from extensive cypress swamp. In farmland, on road beside a drainage ditch bordered by thickets of honeysuckle and canebrake. In deep swamp, on road bordered on one side by deep drainage ditch and on the other by eight-foot-high impenetrable canebrake. Dirt road beside drainage ditch. Coiled on boards of bridge over drainage ditch, near sawdust pile overgrown with honeysuckle, cypress swamp beyond it. (Extracted from unpublished field notes of Barry Rothman and Norma Rothman.)

Ohio: "It frequents low swampy places in hilly regions." (Morse, 1904:137.) ". . . in a variety of habitats . . . almost anywhere in unglaciated Ohio. . . . in the valleys (sometimes along the streams) . . . hillsides to their summits and out over the farm land or woods on the flat-topped hills. Sometimes they were in cleared open country and sometimes in heavy woods, but more often they were taken in scrubby second-growth or brush." (Conant, 1938:110.)

Indiana: "hilly locations . . . common where there is timber with rock outcrops." (Minton, 1944:474.) "Dry, rocky wooded ridges are the preferred habitat, and the species may be quite numerous locally." (Minton, 1951:318.)

Illinois: "The copperhead is most generally found in rocky, wooded areas, although it seems to like the proximity of water, perhaps because of the greater abundance of food." (Necker, 1939:36.) ". . . common only in wooded, rock areas." (Smith, 1953:5.)

Kentucky: (Mammoth Cave region) "Abundant, especially in damp woods." (Hibbard, 1936:281.)

Tennessee: ". . . high, dry and rocky regions. . . ." (Allyn, 1937: 220.) ". . . wooded uplands and hills. None have been found in lowlands or river bottoms." (Parker, 1948:28.) "It is most likely to be encountered in woodlands since it has a preference for hilly or low mountainous country." (Gentry, 1956:248.)

Alabama: ". . . frequents rocky territory, often being found by turning over boulders." (Haltom, 1931:94.)

Mississippi: (George County) ". . . swampy type of country near Basin. . . ." (Allen, 1932:2.) (Jackson County) ". . . . specimens were taken in a deciduous woods of an unusually mesophytic nature for that region of pine meadows." (Smith and List, 1955:123.)

Iowa: ". . . wooded, rocky bluffs on the Mississippi and lower Des Moines rivers. . . ." (Bailey, 1941:1.)

Missouri: ". . . moderately common on rocky hillsides near streams. . . . often taken about dwellings. . . ." (Boyer and Heinze, 1934: 198.)

Louisiana: (northeastern "Hill Parishes") ". . . most abundant in woody glades which lead back from swamps into the highlands. They are not uncommon, however, in swamps and marshes overgrown by trees. During the late summer they are frequently found in paths which border cultivated fields or wooded pastures. Habitat distribution was as follows: woody glades, 25; wooded swamps, 22; paths-field, 9; paths-pasture, 5." (Clark, 1949:258.) (Vernon Parish) "wooded bottomland" (Fitch, 1949:89.) (Lafayette Parish) "rare" in Highland Woods habitat, not recorded at all in the three other habitats listed, namely Swamp, Flood Woods, and Grassland. (Liner, 1955:41.)

Nebraska: (Richardson County) ". . . common along the heavily wooded Missouri River bluffs immediately south of the mouth of the Big Nemaha River." (Hudson, 1942:83.)

Kansas: (Riley County) ". . . among the rocks and vegetation beside riffles of Wildcat Creek. They have also been found under flat, hillside rocks and in grassy, wooded bottom land." (Burt, 1927:8.) (Doniphan County) "among rocks on the bluff . . . under a pile of cottonwood slabs." (Linsdale, 1927:81.) ". . . wooded areas, generally on hillsides where rock is exposed. . . . Extremely heavy woods are not inhabited, for there is insufficient penetration of the sun between the trees to warm the snakes in spring and fall." (Smith, 1956:306.) (Osage County) Oak-walnut hillside forest, cultivated field, Buckbrush-sumac and Prairie habitats found to be used, in that order of preference. (Clarke, 1958:23.) "It is most frequently found in the vicinity of rocky ledges in oak-hickory woods. . . ." (Clarke, 1959:7.)

Oklahoma: (Tulsa County) ". . . rocky, wooded bluffs and ridges." (Force, 1930:37.) (Marshall County) " . . . more common in the postoak-blackjack oak uplands than in the lowlands." (Bonn and McCarley, 1953:470.)

Texas: ". . . timber that borders our rivers and creeks; always selecting land that seldom or never overflows. They hide under logs, in decayed stumps, in holes dug by small animals." (Mitchell, 1903:27.) ". . . most common in rocky areas of mountainous country as well as in the wooded bottomlands. During the spring in some parts of the state they are found in numbers along streams and other moist areas where they spend most of the day hidden beneath decaying logs and other debris. . . ." (Werler, 1950:7.) (Terrell County) "Three specimens were taken from the mesquite-creosote association, three from the mesquite-sumac-condalia, two from the walnut-desert willow, 76 from the live oak, and five from the salt cedar association. One . . . was collected . . . in the hackberry association. . . ." (Milstead, Mecham and McClintock, 1950:557.) (Grayson County) ". . . fairly common in the rocky brushland surrounding the lake [Texoma]. . . ." (Bonn and McCarley, *loc. cit.*) Dallas County ". . . wooded areas in hilly and lowland regions . . . in spring it is found most frequently along the river under logs, pieces of tin, and boards." (Curtis, 1949:12.)

In Trans-Pecos Texas the copperhead is represented by several small and disjunct relict populations in the Chisos and Davis Mountains, in canyons where there is mesic vegetation, and in live-oak groves along tributaries of the Pecos River. These far western populations exist partly by virtue of their increased tolerance for xeric conditions. In a typical locality in the Chisos Mountains, in Oak Canyon near its mouth, there is a grove approximately 100 yards long and 20 to 100 feet wide, of willow (*Salix interior*), oaks (*Quercus robusta, Quercus* sp.), walnut (*Juglans rupestris*), hackberry (*Celtis occidentalis*), buckeye (*Aesculus* sp.), persimmon (*Diospyros texana*), fragrant sumac (*Rhus trilobata*) and grape (*Vitis arizonica*). In places there are small accumulations of leaf litter; for the most part the ground is bare and rocky. Even within the grove there is xerophytic vegetation with such typical desert species as catsclaw (*Acacia greggi*) and prickly pear (*Opuntia* sp.). At the time of my visit in July, 1957, many of the larger trees were dead as a result of drought, and diversion of the limited water supply. Largest trees in the grove were oaks and willows approximately two feet in trunk diameter. Some of these canyons have endemic species and varieties of trees (especially oaks) and other plants occurring as relicts, attesting to a long period of isolation since the climate has deteriorated and unfavorably xeric conditions have developed in this general region. Some of the relict colonies of copperheads exist in situations where the habitat is so restricted as to support only a few individuals. In the Chisos Mountains suitable habitat probably totals less than one square mile; in the Davis Mountains there are more extensive scattered groves, mainly of live-oak (*Quercus emoryi*), and the available habitat doubtless totals several square miles.

On the Reservation in Douglas County, Kansas, the areas of rock ledge that are most frequented in fall by copperheads that are preparing to hibernate are also among the most likely spots to find these snakes at any time in summer (Plate 14, fig. 2 and Plate 15). It is obvious that some individuals remain in the vicinity throughout the summer, while others disperse for varying distances. Those individuals that have wandered far from the ledges return at different times. According to the figures obtained from my ten years of live-trapping, activity along the ledges attains a high level in the last week of September, reaches a peak in mid-October and tapers off abruptly in the last week of October and in early November. In autumn when the snakes are concentrated along the ledges there is a thick layer of new leaves on the ground, as throughout September there is some shedding of leaves, and this process continues at an accelerated rate in October until the latter part of the month when few leaves remain on the trees. The layer of loose leaves provides concealing cover which is effectively utilized by the snakes. Even though they are concentrated along the ledges in a density that might represent several hundred per acre, and are mainly diurnal in their activity at this time of year, they are rarely seen. In walking hundreds of miles along the ledges at the time of year when copperheads are most concentrated there, to check lines of live-traps, I have seen the snakes so rarely (except for those actually in the traps) that I would not have realized their abundance. Copperheads become diurnal in autumn when nocturnal temperatures are unfavorably low. Ledges that have southward exposure are optimum habitat, but many that have predominately eastward or westward exposure are just as much frequented on the Reservation, and some that have partly northward exposure are frequented. Favorable characteristics of the ledge itself may outweigh the disadvantage of an exposure that is not optimum for receiving the maximum amount of sunshine.

In summer, when copperheads have dispersed from the ledges, they occupy almost every terrestrial habitat on the Reservation, but are unevenly distributed as some habitats are much preferred over others. Approximately half of the Reservation's area is woodland, and the other half is chiefly grassland, much of which is in process of transition to brush or forest as plant succession progresses (Plate 14, fig. 1). Interspersion of habitats is so great that the home range of every individual copperhead encompasses a variety of habitat divisions. Effort to capture the snakes was most concentrated in those areas that had proven most productive previously. Numerical comparisons of habitat preferences are not possible with the data on hand, but my impressions of the relative degree of use of several habitats best represented on the area are as follows.

1. Most preferred habitats, having concentrated populations of copperheads throughout the summer.
    - *a.* vicinity of intermittent streams, with groves of elm (*Ulmus* sp.), cottonwood (*Populus deltoides*), locust (*Gleditsia triacanthos*), various other trees, brush, including blackberry (*Rubus argutus*) and ground cover of various herbs and grasses.
    - *b.* fence row lined with brush and saplings of elm, osage orange (*Maclura pomifera*), locust, crab apple (*Pyrus ioensis*), and plum (*Prunus americanus*).
    - *c.* vicinity of pond, with grove of willow (*Salix* sp.), and with dense ground cover of smartweed (*Polygonum* sp.), day flower (*Commelina communis*) and rice cut-grass (*Leersia oryzoides*).
    - *d.* upland thickets of elm, locust, osage orange, crab apple, plum, sumac (*Rhus glabra*) and oak (*Quercus prinoides*) at edges of grassland dominated by brome (*Bromus inermis*) or blue-stem (*Andropogon* sp.).
2. Less preferred habitats, having sparser populations.
    - *a.* woods of oak-hickory (*Quercus* sp. and *Carya ovata*) and hackberry (*Celtis occidentalis*).
    - *b.* xeric thorny woodland of osage orange and honey locust with dense undergrowth.
    - *c.* mesic woodland of elm, ash (*Fraxinus americanus*) coffee-tree (*Glymnocladus dioica*), redbud (*Cercis canadensis.*)
    - *d.* weedy pasture, with brome, ironweed (*Vernonia interior*), vervain (*Verbena stricta*) and germander (*Teucrium canadensis*).
    - *e.* fallow fields dominated by weedy grasses, foxtail (*Setaria* sp.), and crabgrass (*Digitaria sanguinalis*).
3. Least preferred habitats, that are generally avoided, or are used only because they are adjacent to more favorable areas.
    - *a.* mesic fallow field in an early stage of succession, with weedy vegetation dominated by giant ragweed (*Ambrosia trifida*) and sunflower (*Helianthus annuus*).
    - *b.* more xeric fallow field, with common ragweed (*Ambrosia artemisiifolia*), three-awn grass (*Aristida oligantha*), and lespedeza (*Lespedeza striata*).
    - *c.* cultivated field, either almost barren of vegetation or with corn or milo.
    - *d.* road.

The extent to which the less favorable areas were avoided was indicated by experience in collecting copperheads while driving over county roads at night, at times when weather conditions were most favorable for the snakes to be active. A ten-mile drive sometimes disclosed one or more of the snakes, but more often none was seen. It is estimated that in the course of a ten-mile drive approximately 25 acres of road were scrutinized, and if copperheads had been as numerous on the roads as they were estimated to be in nearby favorable habitats, more than 100 should have been secured on each such drive.

RANGE AND GEOGRAPHIC VARIATION

The copperhead occurs throughout most of the southeastern one-fourth of North America but is absent from peninsular Florida and enters that state only along its northern edge. The species is confined chiefly to unglaciated regions, but has locally made small scale penetrations into glaciated areas in Massachusetts, Connecticut, southern New York, Pennsylvania, Ohio, Indiana, Illinois, Missouri, Nebraska and Kansas (Fig. 12).

Most records from Pennsylvania are from the southern half of the state and the species is generally absent from the northern tier of counties. According to Smith (1945:70) the copperhead is absent from most of the glaciated areas of the state, but is beginning to penetrate them using the stream valleys as migration routes. He cited 14 records within glaciated areas, including those of Wisconsin Drift, Illinoian Drift and Pre-Illinoian Drift.

In Ohio most records are from the unglaciated area of the Allegheny Plateau or from near its borders, chiefly from within the southeastern quarter of the state or from its southern edge. Recorded occurrences in the glaciated areas are in or near the valleys of large streams (Conant, 1951:109 and 254). The copperhead is distributed over somewhat less than the southern half of Illinois, but with notable northward extensions in the main valleys of the Mississippi, Illinois and Wabash rivers. Except in these main river valleys the species is limited to the part of the state south of the Shelbyville Moraine.

In Missouri the distribution has not been thoroughly investigated, but most records are in the southern two-thirds—near the Missouri River or south of it. Along the Missouri River the range extends northward barely into the southeastern corner of Nebraska. In Kansas the species is limited to the eastern third of the state. It is abundant in several tiers of eastern counties but becomes increasingly scarce and localized farther west. The species reaches its northwestern limit in the Big Blue River drainage of Gage County, Nebraska. In Oklahoma the range is approximately the southeastern half, in oak-hickory woodlands. In eastern Texas the copperhead is generally distributed. It extends west across the central part of the state in oak woodland, and is common on the Edwards Plateau of west-central Texas. Farther west isolated populations occur in live-oak woods along streams in the Stockton Plateau, and in isolated deciduous forest relicts at higher altitudes in the Chisos and Davis mountains of Trans-Pecos Texas.

In general, the copperhead's distribution corresponds to that of the Deciduous Forest Formation or Biome of the southeastern one-fourth of the North American Continent. Most of the Formation's associations, including the Mixed Mesophytic, Western Mesophytic, Oak-Chestnut, Oak-Pine, Oak-Hickory and Southeastern Evergreen (Braun, 1950), are mainly or entirely within the copperhead's range. Only the two most northern associations, the Beech-Maple

FIG. 12. Range of the copperhead, showing marginal and near-marginal records, based upon a map shown by Gloyd and Conant (1943:153) but including additional records from Pennsylvania (Smith, 1945:70), Ohio (Conant, 1951:275), Illinois (Smith, 1953:2), Kansas (Smith, 1956:305), Oklahoma (R. G. Webb, unpublished thesis in the University of Oklahoma Library), Texas (Brown, 1950:212-213; Milstead, Mecham and McClintock, 1950:557), and Mississippi (Allen, 1932:12; Smith and List, 1955:123).

and Maple-Basswood, are largely outside the range, as is the ecotone of "White Pine-Northern Hardwoods" that is transitional to the northern Taiga.

The copperhead's subspecies correspond roughly to the subdivisions of the Deciduous Forest Biome. The southern subspecies, *A. c. contortrix* for the most part coincides with the Oak-Pine and Southeastern Evergreen associations. The northern subspecies *A. c. mokeson* coincides with the Oak-Chestnut, Mixed Mesophytic and Western Mesophytic associations in the East and with part of the Oak-Hickory Association in the West. The western, or broad-banded copperhead occurs chiefly within the southern part of the Oak-Hickory Association. The Trans-Pecos copperhead, *A. c. pictigaster* occurs entirely outside the Deciduous Forest Biome, but in small relict populations coinciding in distribution with isolated relicts of deciduous forest.

The four recognized subspecies differ from each other, so far as known, chiefly in characters of color and pattern that may be adaptive to the different types of backgrounds in the several types of forest climaxes where they occur. The differences are not striking as compared with those in some other species of snakes, but are consistent and well defined. The northern copperhead, *A. c. mokeson,* is characterized as being reddish brown or chestnut, with relatively little contrast between ground color and the superimposed darker markings. The latter are hourglass shaped—constricted mid-dorsally, widened laterally, and have rounded lateral edges. The ventral pattern is of more or less distinct, subcircular blotches. The belly is usually dark, mottled with gray or black. Gloyd and Conant (1943:150) mentioned small or irregular spots between the crossbands in some populations, and their photograph of a specimen from Dutchess County, New York, has this type of pattern, which was not observed in the population that I studied. The snakes of the eastern United States seem to attain much larger size than those from any other region. It is notable that eastern and western populations of *mokeson* are disjunct, separated by the subspecies *contortrix* where the latter extends north along the Mississippi River and its tributary, the Illinois River as far as central Illinois, the northern limit of the species' range in that region.

The subspecies *contortrix* differs from *mokeson* chiefly in paler coloration, pale brown or tan, often with a pinkish tinge. The dorsal crossbands contrast strongly with the paler ground color, but they shade into a paler hue in their central parts. They are strongly constricted middorsally. The belly is pale, not heavily marked.

A. c. laticinctus is bright chestnut, or hazel brown, with strong contrast between the ground color and the darker crossbands. The latter differ from those of *mokeson* and *contortrix* in lacking middorsal constrictions and in extending laterally to the ventrals (with no rounding of their edges), blending with the ventrolateral pattern of three more or less conspicuous spots to each crossband. This subspecies seems to be relatively small in average and maximum size.

A. c. pictigaster (Plate 16, fig. 1) resembles *laticinctus* in its dorsal pattern, but on the ventral surface there are bold and contrasting dark markings continuing as extensions from the dorsal crossbands at both their anterior and posterior ends and with a U-shaped light area enclosing still another dark area on the ventral surface beneath the middle of each dorsal crossband. *A. c. pictigaster* seems to be a dwarfed race; it has one scale row slightly shortened, and on the average has several more subcaudals than have the other subspecies.

There are indications of ecological differences between widely separated geographic populations, but the available information is inadequate to define these clearly, or to show whether they follow subspecific boundaries. *A. c. contortrix* of the southeastern states has often been found in a swampy habitat and prefers situations that are definitely more mesic than those frequented by the western and northern subspecies. Both of the western subspecies, and especially *pictigaster*, are relatively tolerant of xeric conditions, although they are closely confined to woodland—of limited extent in the regions where they occur. Frogs seem to be far more important in the diet of *contortrix* than in that of *mokeson* (at least of its western representative).

BEHAVIOR

Crawling

Klauber (1956:331-350) has described and explained in detail the modes of progression by crawling in snakes, particularly with reference to rattlesnakes. Four distinct types of locomotion are: horizontal undulatory, rectilinear, sidewinding, and concertina. Most snakes are capable of employing two or more of these types of progression. The mode of travel depends on the kind of snake, size of the individual, type of substrate, degree of excitation, and other factors. Horizontal undulatory locomotion is the most prevalent type in the majority of snakes, and is also exclusively used by limbless lizards such as the glass "snake" (*Ophisaurus*). Travelling by this method, the snake's body is thrown into several lateral undulations or waves, conforming in its contours with irregularities in the ground surface upon which it rests. Pressure is exerted simultaneously on the outside and posterior surface of each curve, providing the force which drives the body forward on its course. On a smooth surface where suitable pressure points for pivots are lacking, the snake's lateral undulations are largely ineffectual in causing it to move forward. In horizontal undulatory locomotion the distance gained by the snake is somewhat less than that actually travelled, because of the lateral motion. Each point along the snake's length tends to move along the same undulatory course, but actually the lateral movements are most pronounced in the anterior part of the body and least so in the head region. The mechanics of this type of crawling are complex. In the copperhead crawling is accomplished chiefly by means of horizontal undulatory progression. When there is cause for haste, the copperhead relies on this method exclusively.

More leisurely locomotion may be partly or entirely of the rectilinear type. This mode of progression is especially characteristic of large, heavy-bodied snakes such as boas, pythons, and large vipers. It depends upon the loose attachment of the skin to the body, with a powerful dermal musculature. In typical rectilinear locomotion the snake's body is extended in a straight line and seems to glide forward effortlessly. The weight is not evenly distributed over the ventral surface, but is supported on several well separated points. Along the intervening parts of the body, imperceptibly raised from the substrate, the loosely attached skin slides forward over the body. As each point upon which the weight is borne shifts posteriorly in a flowing fashion, the body is pulled forward within the sheath of skin. In crawling slowly copperheads often have the body extended almost straight, relying largely on the rectilinear type of locomotion. More often a combination of the rectilinear and horizontal undulatory types are employed.

Sidewinding is a third type of progression; it is well developed only in the sidewinder rattlesnake (*Crotalus cerastes*) and in a few species of true vipers, all heavy-bodied snakes specially adapted for locomotion over a smooth surface of loose sand. In this peculiar type of locomotion most of the snake's body is held arched clear of the ground as it glides along with a rolling motion, with only two points in contact at any one moment. The track consists of a series of parallel lines. This type of locomotion is the nearest approach actually attained to that of the "hoop snake" of folklore. The hoop snake was supposed to take its tail in its mouth and roll down hill like a hoop. If a hoop is broken, and the free ends are pulled in opposite directions until the shape is stretched to a spiral with two loops, and if this spiral is rolled over a smooth surface, the motion resembles somewhat that of a sidewinder. The resemblance would be increased if the hoop were made of such flexible material that the loops sagged to an elliptical shape. Although few kinds of snakes use sidewinding regularly, others resort to it in emergencies, as when escaping over a smooth surface unsuitable for horizontal undulatory progression. These kinds include several species of rattlesnakes and even garter snakes, but in most of them sidewinding efforts are crude. In the stubby and clumsy copperhead sidewinding locomotion is never well defined. However, individuals startled as they are crossing roads or other open places with a relatively smooth substrate may make lunging movements, with part of the body off the ground, progressing, though inefficiently, in a manner that may be considered primitive sidewinding or its precursor.

In the fourth method, concertina progression, the snake alternately anchors itself at the anterior end drawing the body forward in several sinuous curves, and then by straightening the body extends itself out full-length anteriorly. In each cycle the snake advances by the difference between the lengths in its straightened and waved positions. Concertina progression is not the regular method in any snake, but is used especially in a slow cautious advance, as in the stalking of prey. I have never seen concertina progression used by the copperhead.

Coiling

The copperhead spends most of its time in a flattened pancake-like coil which is characteristic for the species. In this coil the tail is outermost and the body is compactly wound in from one to more than two complete cycles. Near the anterior end of the snake the direction of the coil is reversed, and the head and neck, near the center, assume a U- or S-shape. From this position the snake is able to strike, in a short jab, but ordinarily, upon the approach of prey or an enemy, it would make preparatory movements including a slight raising of the forebody and a shifting of the coils to bring more of the length into the anterior loop, thus lengthening the potential range of an effective stroke. Ordinarily the snake seeks a sheltered spot in which to coil, concealed under a rock or in leaf litter or in dense growing vegetation. Probably food is most often obtained by snakes that are lying in resting coils, waiting to ambush approaching prey. Before the prey has approached within reach of the snake, the latter is alerted by sight, scent, substrate vibrations, or the radiation receptors of the heat-sensitive pits. The slight movements required to prepare for a stroke would not be readily noticed by the approaching victim.

Copperheads kept in outdoor enclosures were remarkably efficient at concealing themselves in their resting coils. In one pen which enclosed 100 square feet prolonged search was often necessary to find snakes that were not coiled beneath several wooden shelters provided for them. Usually they were found nestled amid screening vegetation. In their compact, flattened resting coils, copperheads presented a minimum surface to be seen, especially by a small animal approaching on the same horizontal plane. Since it was considered desirable to avoid unnecessary disturbance, and since hazard was involved in searching with hands or face near the ground, such snakes were often missing for periods of days. Those kept under observation were often coiled in just the same position over periods of hours, or even for several days. Those that were digesting a meal or were approaching the time of shedding were especially sedentary. From the behavior of these captive individuals under conditions simulating those in the wild it may be concluded that a copperhead often remains for 24 hours or more in the same spot. Movements within the enclosure were often motivated by changing conditions of sunshine and warmth within the daily cycle as the snakes sought to maintain body temperatures near their optimum level.

On many occasions snakes kept in the enclosures were observed to return to the same spot to resume a resting coil after wandering about the cage. Any one spot might be used with some regularity for a week or more, but eventually would be deserted in favor of another. In the cages the number of potential resting places was limited. The nest or "form" shaped by a snake coiled in one place for a long period would naturally provide an ideal site for occupancy on a later occasion. Under natural conditions, with freedom of movement so that the snake wanders much farther in a period of foraging, and with abundant shelter on all sides it is doubtful whether an individual returns to the same spot with any regularity. On the few occasions when I have caught a copperhead twice in the same trap, the interval was short and it seemed probable the snake had blundered back into the trap after release, without having left the vicinity. Otherwise I have rarely found the same copperhead twice at any one spot. It has not been demonstrated whether the occasional aggregations of gravid females have any permanence but from the appearance of one shelter where an aggregation was found, I judge that it had been used for several days at least, and that the individuals involved may have left and returned again.

Copperheads that are travelling move slowly. The motion is so gradual and so smooth-flowing that the snake remains extremely inconspicuous against its normal background, and might ambush prey almost as effectively as when it is in a resting coil. The rate is of course variable, but would be measured in yards per hour rather than in miles per hour. The crawling snake is seldom in motion for more than a few seconds without stopping for a longer or shorter period. Usually much more time is spent in the intervals of pausing than in motion. The route is usually circuitous.

Swimming

Unlike its near relatives, the cantil and the cottonmouth, the copperhead has no special affinity for water. However, it does favor damp situations and many authors have mentioned its preference for mesic or riparian habitats. In captivity copperheads have been observed to coil in the water containers in their cages, in response to air temperatures that were either uncomfortably high or uncomfortably low. Like most snakes, the copperhead swims well and occasionally it enters the water voluntarily. In Pennsylvania, Hudson (1954:72) recorded one found swimming across Unami Creek. Smith and Sanders (1952:214) noted one swimming across Lake Texoma, 500 yards from the Texas shoreline.

Climbing

Although it is obviously lacking in scansorial adaptations, the copperhead, like various species of rattlesnakes, has on occasion been recorded climbing in trees or bushes. Those I kept in an outdoor enclosure sometimes climbed several feet off the ground in vines that were intertwined through the wire on the sides of the cage. Of the two Trans-Pecos copperheads that I collected at Independence Creek, Terrell County, Texas, in June, 1957, one was climbing two feet above ground among the roots of an uprooted live-oak. Wright and Wright (1957:916) mentioned an individual of this subspecies found coiled in the fork of a live-oak four feet above the ground in the Davis Mountains. Vernon Mann told me that his brother was bitten when he placed his hand in the crotch of a tree six feet above the ground and unknowingly touched a copperhead that was inconspicuously coiled there. The Marais des Cygnes River of Kansas had flooded the woodland where this accident occurred, and probably the copperhead had climbed into the tree to escape the rising water. Johnson (1948:214) wrote of finding a half-grown copperhead coiled in the uppermost branches of a small tree on July 10, 1948, in McLennan County, Texas, and on other occasions found individuals four to five feet above ground level in piles of driftwood. Swanson (1952:176) mentioned finding several young copperheads climbing in laurel bushes a foot or more above the ground, in Venango County, Pennsylvania. Curtis (1949:12) wrote of finding several copperheads in Dallas County, Texas, climbing in low shrubs and trees after dark in mid-July, ostensibly to catch cicadas. Wm. Cutter told me of making similar observations in Marshall County, Oklahoma. When cicada nymphs are emerging from the ground in large numbers, and climbing stems and tree trunks, ready to metamorphose, copperheads may be stimulated by sight, scent or sound to climb after them, abandoning their usual tactics of waiting in ambush, in favor of active pursuit. The nymphs, and the newly metamorphosed adults of cicadas that are not yet completely dry, are so slow and clumsy that, unlike most prey, they could be readily overtaken and caught, even by the slow-moving copperhead.

Judging from a few brief statements in the literature, some other species of *Agkistrodon* have the tendency to climb more strongly developed. Smith (1943:500) considered *A. hypnale* of India to be partly arboreal as it often climbs into low bushes. Koba (1938:247) studied an insular population of *A. halys* off the coast of southern Manchuria, and found that these snakes often climbed into trees or weeds, and fed mostly on birds.

Disposition

Widely different opinions have been expressed in the literature as to the copperhead's disposition; some writers have described the species as docile and inoffensive whereas others have considered it the personification of villainy. Atkinson (1901:152) described the copperhead as a ". . . sullen and treacherous snake, its disposition is to remain concealed and it will not strike unless closely pressed or trod upon." Mitchell (1903:27) wrote of copperheads in Texas that they were rather lazy and sluggish until thoroughly aroused, but then became vicious. Branson (1904:421) wrote that in Kansas, "It strikes without warning and seems to be always on the lookout for something upon which to use its fangs." Morse (1904:137) also wrote, "It strikes, when approached, without warning. . . ." Surface (1906:186) wrote, "There is no creature more treacherous, despicable nor dangerous in this State [Pennsylvania] than the Copperhead Snake. It lurks in bushes or grass or among stones, and strikes without warning and often without provocation." However, Brimley (1923:114) wrote that it is a "gentle snake, much less aggressive or vicious . . . than most of our harmless snakes." Amaral (1927:70) stated that the copperhead is a rather vicious snake and strikes in any direction without warning. Babcock (1929:26) described the copperhead as having a ". . . shy and retiring nature, rarely becoming aggressive." Ditmars (1935:23) averred that it would seldom strike unless stepped upon, or otherwise attacked or annoyed. In Indiana, Minton (1944:474) noted marked individual differences in temperament and wrote that individuals had been touched or even trodden upon without striking, whereas others would strike with but little provocation. McCauley (1945:132) wrote, "I have never seen a truly aggressive specimen." Oliver (1958:45) wrote that most copperheads are quite mild and inoffensive.

My own observations in general bear our Oliver's statement. In the many encounters with copperheads experienced by my associates and by myself on the Reservation, the snakes never behaved aggressively, but would attempt to defend themselves only when they were threatened or restrained. Even under these conditions the snakes sometimes did not strike or struggle when they were held down, grasped, and handled. When I discovered a copperhead in a funnel trap, I would remove the end of the trap and shake out the snake onto the ground. Usually the snake drew back into a coil and remained almost immobile until I was ready to handle it, but upon being grasped it would struggle to gain its freedom by writhing and thrashing, emitting jets of musk, voiding the contents of the cloaca, and making vigorous attempts to bite.

An occasional copperhead found foraging at night away from shelter, showed more animated defensive behavior and even attempted to regain the nearest shelter by moving toward me with threatening lunges. Besides lack of the rattle, other sematic behavior—hissing, inflating the body, assumption of menacing posture with much of the body held clear of the ground, protrusion and slow, waving motion of the tongue—is much less developed than in rattlesnakes. Hence the accusation that copperheads strike without warning is not wholly unfounded. On one occasion, as I removed the dry grass covering a funnel trap, a small copperhead inside struck against the wire, and one fang scratched my knuckle. The only preliminaries to delivery of a bite may be a quick cocking of the head toward the disturbing object, and perhaps a slight shifting of the coils.

No effort was made to make pets of the copperheads that were kept in captivity from time to time, but such individuals even if born in captivity, remained unpredictable in disposition, and any attempt to handle them without the usual precautions would have been foolhardy. Although well adjusted to the presence of persons in the room where the cage was kept, the snakes were easily annoyed by any disturbance near their cage, and would prepare to strike or, on occasion, would strike against the screen or glass side of the cage at a nearby object.

Both in confinement and under natural conditions there were fairly consistent differences in temperament between the sexes. Males, especially older individuals were more irritable and aggressive. Gravid females were much more docile than were other copperheads.

Combat Dance

The so-called combat dance has long been known in snakes, but until recently it was most often misinterpreted as mating behavior. Klauber (1956:671) expressed the opinion that the combat dance had only occasionally been mentioned in the literature because observers had nearly always assumed the intertwined snakes were actually mating, and may have avoided the subject, except in "the more Kinsey-like types of scientific publications." However, judging from the frequency with which the sexual behavior of snakes has been described in the literature, the combat dance must be a relatively rare phenomenon.

Combat dance has been described in many kinds of snakes, including colubrids, elapids and viperids, but seems to be best developed and most often observed in the crotalids, in which it has been well described by Shaw (1948:145), Gloyd (1947:3), and Klauber (*loc. cit.*). A typical combat dance occurs when two adult male crotalids (nearly always of the same species) meet, and one, more aggressive, challenges the other, which accepts the challenge.

Facing each other the two snakes rear with their forebodies erect in a posture reminiscent of that of an angry cobra. As they come together their ventral surfaces are firmly adpressed, and the support thereby gained permits each snake to rear higher than it could otherwise. Swaying unsteadily in this position they intertwine their necks with slow, writhing movements, until one snake, momentarily gaining a favorable position, suddenly and violently contracts its body against the other in such a way that the opponent is thrown off balance and hurled forcibly against the ground. The snake that has thrown the other may follow up its advantage by moving onto the opponent and pressing him against the ground, thereby hindering and delaying his recovery, but the struggle, once joined, usually continues through many falls, with the same individual consistently playing the part of aggressor. In observed instances no perceptible damage to either opponent has resulted. Eventually one of the combatants may become discouraged and failing to respond to a renewed challenge, moves off whereupon the other does likewise without molesting him further. In captivity individuals that have engaged each other in combat dance are likely to repeat the performance frequently over periods of weeks.

The true significance of the combat dance, and its motivation are still poorly understood. In a few observed instances a female has been present when males were struggling, but most often, both in captivity and under natural conditions, no female was present and it seems unlikely that the combat is motivated primarily by sexual rivalry or to establish priority in mating. Sutherland (1958:23) related an instance of two adult males of the timber rattlesnake in captivity engaging in combat dance after both had grasped the same morsel, a dead blackbird, and each was obviously angered by the other's attempts to appropriate the meal. After one snake was vanquished, the other returned and ate the bird. On a later occasion Sutherland observed a smaller rattlesnake and a copperhead both interested in the same mouse. "They exhibited extreme agitation, inflating their bodies, emitting musk and weaving about with bodies elevated and necks arched." Unfortunately on this occasion one of the snakes was distracted by another mouse before there was opportunity for a typical combat dance.

Somewhat similar behavior was described by Sutherland (*in litt.*) in a male copperhead whose courtship was interrupted. "While the male was courting, the observer gently stroked his body with a pair of long forceps. The male became agitated and moved spasmodically. He inflated his body, emitted musk, and arched his neck. His movements became more violent with each stroke of the forceps, until the anterior part of his body was elevated six or eight inches above the floor of the cage. The same behavior pattern was demonstrated when another snake crawled over his body in the course of the courtship. Generally he returned immediately to the female when he was left undisturbed after these interruptions."

Charles E. Shaw, in a letter to Sutherland, expressed the idea that the dance was an exhibition of, and a defense against, homosexuality. Support for this idea is to be found in Shaw's (*loc. cit.*) account of the dance in rival male rattlesnakes (*Crotalus ruber*). The contest began after one male crawled onto the other, lying along him, facing in the same direction in a position similar to that assumed in mating. The lower male then raised the anterior third of his body and turned to face the opponent, who then also raised his forebody.

Gloyd (*loc. cit.*) quoted the observations of Mr. Joseph Ackroyd made on two male copperheads near Winchester, Virginia, in late July, 1945, as follows: "The dance took place at 10:30 P. M. at the side of a farm lane bordered on one side by an uncleared fence row and wild blackberry patch and on the other by a long, wild meadow sloping down to a small stream across which is a woods of second-growth oak; elevation approximately 800 feet. . . . Possibly two-thirds of the anterior portions of the snakes' bodies were entwined vertically with the exception of a portion of the neck. The heads were opposite each other and there was a slight swaying movement between them. About one turn of coil was wound and unwound, first in a clockwise and then in counter-clockwise direction. At no time did the distance between the heads change during the rhythmic movements, and at no time did the snakes progress along the ground. It seemed as if the posterior ends were definitely 'anchored'. On three distinct occasions one of the snakes broke the rhythm of the dance by darting its head rapidly at the other."

Shaw (*loc. cit.*) having observed the dance in captive copperheads, stated, "The combat dance of *Agkistrodon m. laticinctus* is similar to that of *Crotalus* but differs quite markedly, insofar as our observations are concerned, in that one of the males acts as though he were afraid of being bitten on the head. . . . always ducks and dodges the head thrusts of the aggressor . . .

although the aggressor never attempts to bite. . . . These snakes also seem to be more tensely alert during the dance, and the neck-twining motions much more hurried, contrasting with the comparatively leisurely motions observed in *Crotalus*."

Mr. Delmer Ferguson of La Cygne told of seeing two large copperheads engaged in combat "dance" in a road near his home. He was not able to describe any details since the incident had occurred many years before. I have never seen a typical combat dance, either under natural conditions or in captivity. On September 26, 1957, the two males in a litter of copperheads born in captivity only four days earlier, slowly approached each other, with their heads and necks elevated, and as they met, they reared until in each approximately the anterior 2/5 extended up vertically from the substrate. Their ventral surfaces were pressed against each other, each one supporting the other's weight. The snakes remained balanced in this position for almost a minute. Although no evident hostility or combat was involved, the behavior seemed to be akin to that of the combat dance in adults.

The nocturnal habits of the copperhead perhaps explain in part, why the combat dance has so rarely been observed in such a common species. In captivity normal behavior seems to be largely inhibited in most individuals. The combat dance was not observed in the outdoor enclosure where several males were kept together and behaved more normally than those in closer confinement. In my opinion the combat dance is a rather rare phenomenon even in the wild, evoked only in certain individuals under special conditions.

SHEDDING

The skin may be shed within a few days after birth but the interval is variable. Gloyd (1934:600) found that ordinarily all young of a brood shed about the same time, most often on the seventh or eighth day, but the range was from three to ten days. Chenoweth (1948:162) recorded a litter of five copperheads born on September 4 in which all shed on September 10. In two litters kept by Conant (1951:112) the young shed from five to ten days after birth. In litters kept by me shedding usually occurred within the time range indicated by Gloyd, Chenoweth, and Conant, but it was sometimes delayed and under unusually dry conditions sometimes did not occur for several weeks. After such delayed shedding the slough did not come off entire and there was a tendency for patches to remain. Some young had to be soaked for a day or more before they were able to shed. Especially in the stunted young born from undernourished females, shedding was liable to be delayed beyond the normal time. Young that did not shed promptly perhaps tended to outgrow their skins as they increased in length, living on the stored yolk. They became increasingly handicapped in their movements as they were stiffened by the dry layer of outer skin. Such young were unable to assume the characteristic compact resting coil, but usually lay with their bodies extended, either straight or with only minor flexures. In individuals less affected, and able to coil, the decreased flexibility of the skin was shown by bends or creases in the concavities of the coils. Probably feeding of young is delayed in most instances until shedding is completed. Even in their locomotion, and in striking to defend themselves, the young are handicapped by the stiffening effect of their unshed skins. After shedding, the young are far more alert and active; they may take food, and when quiescent they nearly always assume the typical resting coil.

Copperheads that have recently shed have their patterns unusually bright and vivid. Those that are preparing to shed are unusually dull and dark in appearance. However, the approach of molt is less evident than in some other kinds of snakes and the eyes do not assume the milky opaque appearance characteristic of many snakes. When the molt is approaching, the snake is unusually sluggish. In captivity, even those individuals that feed well at other times cannot be induced to take food when shedding is imminent. Immediately after shedding the snake shows renewed animation, moves about more than usual, and is eager to feed.

Stabler (1939:228) presented data concerning the frequency of shedding in many species of common snakes that he kept in captivity. One copperhead shed eight times in 24 months. Excluding a "rest period" or pseudo-hibernation that occurred in the poorly heated room where his snakes were kept from early October to April, Stabler obtained a figure of 1.8 months as the average interval between molts for this snake. Ahl (1930) recorded two molts in a copperhead kept for 12 months, and Carr (1926:150) recorded six molts in one that was kept 11 months and fasted throughout the entire period.

Obviously the frequency of shedding varies and is influenced by many factors including the size and age of the individual, the amount of food that it consumes, and the temperature. Most of the copperheads captured in the course of my field study were marked with a daub of brightly colored enamel paint before they were released, in an attempt to gain information concerning the frequency of shedding. Those retaining the paint at a later capture were known not to have shed in the interval. Nevertheless, the data obtained regarding shedding were remarkably meager. Most of the snakes recaptured were taken after intervals too long or too short to yield significant information regarding shedding. In warm, damp weather the paint tended to crack, peel, and wear away as the snakes crawled through ground litter and dense vegetation. After several weeks little or no paint might remain, even though no molt had occurred. Therefore, only the positive evidence provided by retention of the paint from one capture to the next was definitive.

Most individuals caught after intervals of up to two weeks retained their paint. An adult male marked on September 27, 1958, retained paint when caught 37 days later, and a large adult female marked on June 20, 1958, likewise retained paint after 49 days. A small adult male marked on October 23, 1957, retained paint after seven months when recaptured on May 21, 1958, but this interval was mostly winter dormancy with probably not much more than a month of active existence. As opposed to these three positive records, copperheads that had lost their paint were recaptured after the following intervals, in days: 39, 40, 41, 45, 51, 54, 57, 61 and 61. Also many longer intervals were recorded.

In rapidly growing young copperheads in captivity I recorded molt intervals of 31, 32, 34, 35, 41, 57 and 70 days, and, in an adult, 63, 85, 89, 94 and 96 days. The young that shed in 31 to 34 days were first-year individuals that were being fed maximal amounts and were making unusually rapid growth. The average interval of 85 days obtained for the captive adult may be typical of individuals under natural conditions.

The many gravid females that were kept through September in order to obtain litters, mostly shed within three weeks after birth of their young. Whether shedding occurs regularly in the entire population at this season, or whether shedding is in part controlled by the physiology of the reproductive cycle was not determined. The sloughed skins are rarely found under natural conditions. They are often cast in burrows of rodents or deep rock crevices where they would usually be overlooked.

Adults probably shed two or three times in the course of their season of activity, and juveniles probably shed three or four times in their first full growing season.

HIBERNATION AND THE EFFECT OF TEMPERATURE

In the region of the Reservation copperheads spend at least half the annual cycle in hibernation, which normally extends from some time in late October or early November to some time in April. Earliest recorded dates of emergence in the 10-year study were: April 15, 1950; April 24, 1951; April 23, 1952; April 8, 1953; April 25, 1954; April 20, 1955; April 5, 1956; April 25, 1957; April 13, 1958; and April 6, 1959. Latest dates of record were: October 27, 1949; November 14, 1950; November 20, 1951; November 12, 1952; October 31, 1953; November 16, 1954; November 2, 1955; November 15, 1956; November 23, 1957; November 14, 1958; and November 5, 1959. The average dates indicated by these figures—April 17 for emergence and November 11 for retirement—represent the extremes; most individuals emerge later and retire earlier. The figures for spring emergence are mostly based upon individuals found under rocks, and at this season the snakes spend much time basking under large rocks that are warmed by the sunshine on warm days but provide sufficient insulation when the temperature is low. In autumn, the snakes rarely frequent such situations but tend to seek out deeper shelters that will serve as hibernacula. The autumn records are therefore based either upon individuals found in the open or those live-trapped at the hilltop ledges. For the latter, the date used is not necessarily the date on which the individual was found in the trap. Often the traps were checked on days too cold for the snakes to be active above ground. Snakes found in the traps on such days were known to have been caught in warmer weather, one or more days earlier. In April, early May, late October and early November temperatures are often too low for the snakes to be active. Some individuals are dormant throughout these periods, while others are active intermittently when the temperature is sufficiently high.

Copperheads are especially gregarious at the time of hibernation. Vernon Mann of La Cygne, Kansas, told of collecting several thousand copperheads, mostly at their hibernation sites, over a 30-year period. The dens were at tops of bluffs in rocky situations that were hotter and drier than the surrounding habitats, usually where the exposure was mainly to the south. At times of emergence he found the snakes scattered along the ledges; rarely as many as 30 were found in the vicinity of one den entrance. On various occasions Mann had attempted to dig out dens but had never succeeded, as the dens were always deeper than anticipated, and were among rocks. On one occasion, he dug down through loose shalelike rock to a depth of more than four feet, whence the tunnel led beneath a massive boulder and could not be followed farther.

Mann thought that the snakes sometimes travelled as much as two miles to and from the hibernation sites but that most travelled shorter distances. He thought that regular travelways existed between denning areas and summer ranges. He mentioned so-called "snake rocks" along such routes which might shelter as many as six copperheads at one time. Presumably trailing by scent would account for such aggregations.

In several different years I have first found copperheads in spring at the hilltop ledges under large flat rocks where there were deep crevices that probably led to hibernacula. On April 6, 1959, for example, after several hours' unsuccessful search, I turned a flat rock approximately 20 inches in diameter and three inches thick, and found an adult copperhead in damp soil beneath. A second was coiled in contact with the upper edge of the rock partly concealed beneath dry leaves. Raking through the heavy leaf litter that had accumulated on the uphill side of the rock, I uncovered two others. Thorough search failed to reveal any more in the vicinity. A round hole one and a half inches in diameter extended downward almost vertically from the depression from which the rock was moved. As it seemed almost certain that the copperheads had emerged from this hole, I attempted to excavate it. The diameter of the tunnel enlarged to several inches, and the hole deviated slightly from the vertical, slanting back into the hillside until it contacted a vertical rock face, of the Toronto Limestone. At a depth of 16 inches the cavity divided into two almost horizontal branches running in opposite directions along the rock face. One branch was traced for approximately six feet and the other for four feet, but excavation had to be abandoned because of massive limestone slabs and boulders, wedged in crevices or too heavy to be moved. However, it seemed that the cavity extended indefinitely in both directions along the rock face, and that it was formed by pulling away of the loose soil, tending to slough downhill from the outcrop, with subsequent filling of the upper part of the crack by compacted dead leaves and other accumulated debris eventually forming a soil layer. Soil in the supposed den cavity was moist from seepage trickling over the face of the outcrop.

At the time the snakes were found, in mid-afternoon, temperature was 80° F—the highest of the season up to that time. Successive maxima on preceding days had been 73°, 74°, 55°, 79°, 70°, and 70° (on March 31). On still earlier dates maxima usually were not above 60° (except for March 23 and 24 with maxima of 74°), and it is doubtful whether any copperheads had been active. Of the four copperheads found on this occasion, one was a small adult male, two were adult females, and one was a subadult female. The male was in breeding condition and one of the adult females had semen in her cloaca, indicating that copulation had occurred recently, perhaps on the day that they were found. On the night following capture of the snakes there was a cold front with heavy snow, and freezing temperatures were frequent in the following week. Not until April 15 was temperature again high enough (70° F) for emergence. On April 16 also weather was mild, but another week of cool weather followed, and it was not until April 23 that mild weather returned. Probably many copperheads did

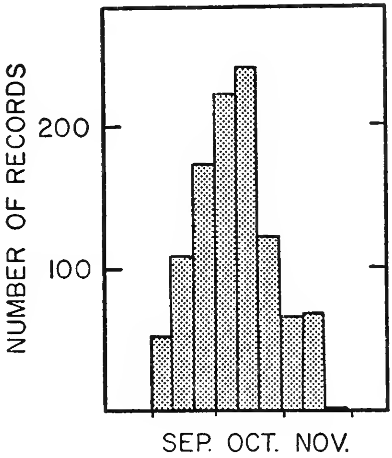

FIG. 13. Numbers of copperheads caught along hilltop rock ledges in autumn, in area shown in Fig. 1, grouped in ten-day intervals. Eleven years' data are combined, but the trends differed slightly from year to year. In general the trends reflect amount of activity of the snakes along the ledges, but trapping effort was somewhat less in early September than it was later in the autumn. In a typical year, activity along the ledges increases throughout September and until mid-October, then activity tapers off abruptly.

not emerge at all until after this date. Changeable weather with temperatures often below the threshold for activity in copperheads, is typical of April in the area of my study, and much of the month is spent in dormancy in most years.

Noble and Clausen (1936:314) excavated a hibernation den near Stony Point, New York, in January, 1933. The twenty-one copperheads dug out of crevices in the rock ledges were encountered singly or in groups of two or three within an area twelve yards square and about four feet from the surface. Minton (1951:322) stated that in southern Indiana copperheads hibernate on wooded, rocky hillsides. McCauley (1945:132) mentioned the tendency to seek hilly rock-ledge areas for hibernation but cited an instance of 37 being found in early spring in a manure heap where they probably had spent the winter. In Richmond County, Georgia, Neill (1948:112) found that not all copperheads frequent regular dens to hibernate. He sometimes found them hibernating beneath pine stumps or under the bark of stumps. A large den where many hibernated was located on the outskirts of Augusta, in a rocky outcropping bordering a golf course. Corrington (1929:58) found two copperheads hibernating in a log near Columbia, South Carolina. Similarly, Strecker (1935:26) found four hibernating in a hollow pin-oak log in McLennan County, Texas.

Dundee and Burger (1948:1) found a denning area of copperheads in Rogers County, Oklahoma, extending for about a mile and a half along a bluff of limestone and sandstone. Coachwhip snakes (*Masticophis f. flagellum*) and western cottonmouths (*Agkistrodon piscivorus leucostoma*) were also numerous along the bluff on April 5 and 6, 1947, when the observations were made. The three species were found together to some extent, but differences in preferences of denning sites were evident. The copperheads were concentrated in drier areas, usually the east and southeast exposures of the bluff. The cottonmouths were concentrated on northeast facing slopes that were damp from seepage. The coachwhip snakes were found in more open areas than those occupied by the copperheads and moccasins.

On the Reservation many species of snakes hibernated in dens formed by crevices and fissures in the hilltop rock outcrops, which totalled 9.1 miles on the area. Different species were found most concentrated at different stages of the season, but no segregation according to habitat was apparent. Most species spent the summer in other habitats, converging on the ledges in fall and dispersing again in spring. All species favored south- or southwest-facing exposures and tended to avoid exposures that faced north. The yellow-bellied racer and red-sided garter snake, two of the commonest species, were often found in the same traps with copperheads, and doubtless often hibernated coiled together with them in the same shelters. Less frequently the black rat snake, timber rattlesnake, blotched king snake, milk snake, and common water snake have likewise been trapped with copperheads. In all the instances of double or multiple captures with different species involved, there were no injuries to either kind of snake. The association of the garter snake and racer with the copperhead in hibernation is of special interest because each of the three occasionally preys upon young of the others in summer. In autumn, when the snakes gather at the ledges there is no hostility, and in hibernating groups, regardless of the species involved, each individual may benefit from contact with the others in maintaining favorable conditions of temperature and humidity.

The timber rattlesnake, sharing most of the copperhead's geographic range, and having similar habitat preferences, is a frequent associate of the copperhead in denning areas. On the Reservation the timber rattlesnake is relatively scarce, but most of those found are trapped in October along the same rock ledges where copperheads are most abundant. In several instances a rattlesnake and a copperhead have been caught simultaneously in the same trap. Klauber (1956:567) quoted B. A. Eger of Buena Vista, Virginia, who had found copperheads and timber rattlesnakes coiled together in dens in cold weather, and Stephen H. Harwig of Pittsburgh, Pennsylvania, who had found numerous copperheads and some pilot black snakes at the same "den rock" with timber rattlers in summer, and believed that all three denned together to some extent in winter. Swanson (1952:176) found three young timber rattlesnakes and ten copperheads together at a den near Mt. Alto, Franklin County, Pennsylvania, on September 28, 1924. Klauber mentioned a newspaper account of a den that contained 193 adult timber rattlesnakes, 16 black snakes and a copperhead. The same author (*op. cit.*:551) quoted John H. Stanley of Andrews, North Carolina, mentioning an instance of 30 adult timber rattlesnakes and copperheads killed at one time by dynamiting a den on the Pisgah National Forest. Noble and Clausen (*loc. cit.*) found eight timber rattlesnakes with the aggregation of 21 copperheads excavated from a den near Stony Point, New York. Two racers (*Coluber constrictor*) were nearby.

Hudson (1942:83) mentioned the finding of mixed dens of hibernating timber rattlesnakes and copperheads in the course of quarrying operations in Richardson County, Nebraska.

In January, 1954, a thermometer was installed 33 inches deep in a rock crevice at the base of a limestone outcrop near the top of a south-facing slope. Copperheads were known to hibernate within a few yards of this spot, but depths of the hibernacula were, of course, not known. Even in bitterly cold weather of midwinter, the temperature in the crevice never fell below 3° C.; for most of the season of dormancy it ranged between 4° and 11°. During the latter half of summer and early autumn the temperature remained near its maximum level, usually between 20° and 21°. From January through most of July there was a fairly consistent warming trend, and from mid-October through November, December and January the reverse trend was noticeable.

In the winter of 1956-57 copperheads were kept in a hibernation box one foot square and six inches deep, sunk 30 inches underground. A plastic tube two inches in diameter led from the box to the soil surface at an angle of approximately 30°. An insulation box filled with sawdust was on top of the hibernation box, which also contained a maximum-minimum thermometer. The interior of the hibernation box could be readily inspected by lifting out the insulation box and removing the lid. On November 18, 1956, when temperature was 8.8° C., two adult copperheads and two young of the year were placed in the box. None of the copperheads survived the winter in this artificial hibernaculum. The box was opened from time to time in the winter when air temperatures were well above freezing. On these occasions notes were taken, as follows.

November 30. Air 11.4°, interior of box 9.5°, the minimum reading up to that time. Snakes sluggish but not dormant, and shifted position slightly as the box was opened.

December 16. Air 6.7°, interior of box 5.7°. Copperheads all coiled together; shifted coils slightly when lid was removed from box. One was removed from the box momentarily for observation. It could barely move but was too stiff to attempt to bite and could be freely handled with impunity.

December 26. Air 11.1°, interior of box 8.3°; snakes did not move when uncovered.

January 2. Air 3.9°, interior of box 5.5°. The copperheads did not move until touched. When removed from the box, they seemed aware of their surroundings and responded to stimulation with slow squirming movements, but were unable to defend themselves. Even when touched on the head they usually did not attempt to bite. When so stimulated, one did open its mouth, but seemed unable to coordinate its movements for biting. They lay quiescent except when placed near to cover; then, with slow, clumsy undulations they attempted to gain shelter.

January 12. Air 4.4°, after passage of a cold front with minimum of —9.7°. Interior of box 6.7°, up from a minimum of 5.0°. As before, the snakes were slow and sluggish but not completely dormant.

January 19. Air 7.8° after a period of much colder weather. Interior of box 3.9°, the minimum reached up to that time. A copperhead that was near the top of the box drew back on the defensive as the lid was removed.

January 21. Air 20.4° after arrival of a "warm front"; interior of box 6.1°, up from a minimum of 4.5°.

February 8. Air 13.3°. Interior of box 4.4°.

February 16. Air 10.0°. Interior of box 3.3°.

February 27. Air 10.7°. Interior of box 4.4°. Two of the copperheads were dead. One of these, an adult that weighed 129.8 grams when placed in the box, had declined to 98.6 grams. Perhaps part of the weight loss had occurred after death. Approximately six inches of this snake's head and forebody were in the exit tube, but the head was turned back toward the box. Dissection revealed the snake's lungs to be inflamed.

March 12. Remaining adult copperhead found dying on ground surface beside the entrance hole leading to the hibernation box. When stimulated, its tail twitched slightly, but it was incapable of any other movement. Obviously it had been caught out and frozen on the preceding night when temperature had been several degrees below freezing. The entrance hole of the plastic tube leading to the hibernation box was partly plugged, and the snake probably had been unable to gain entry. On March 11, weather was mild with a maximum of 20°, and the snake had probably emerged on this date. Just what stimulus impelled it to leave the hibernaculum is not clear, since temperature within the box varied but little throughout the winter. The temperature range within the box was similar to that in the natural crevice where a thermometer was installed 33 inches deep at the base of a hilltop outcrop.

Copperheads released from live-traps at 10° C. were capable of vigorous movement. When dropped beside a rock crevice, such a snake would escape into it, moving briskly but rather stiffly. When handled, the snake would attempt to escape and to defend itself, in a slow-motion version of the usual behavior, writhing, thrashing, throwing the body into the characteristic kink, and attempting to bite. However, if released away from the immediate vicinity of shelter, the snake tended to lie motionless indefinitely, without attempting to escape or defend itself unless it was actually touched. On April 21, 1959, I found a copperhead among dry leaves emerging from the entrance of what appeared to be a mammal burrow—an enlargement of a deep crevice in a hilltop rock ledge. Its oral temperature was 14.3°, but the cloacal temperature was only 10.2°, perhaps still near the temperature in the hibernaculum from which it had recently emerged. The foreparts had warmed more rapidly as the slowly emerging snake came in contact with the warmer surface air and, perhaps was warmed slightly by insolation although the sky had been mostly overcast. Probably 10° C. is near the threshold temperature at which torpid copperheads may rouse themselves to activity. On April 23, 1952, a copperhead was found in the open when air temperature was 11.6°. Bodily temperature of the snake itself was higher as it was basking in sunshine, but presumably it had become active and left shelter at an air temperature near 11°. On October 29, 1957, two copperheads were found in funnel traps where they had been caught on one of the two preceding days when temperatures reached maxima of 12.8° and 10.5, respectively. Even at such low temperatures snakes may be sufficiently active to respond to heat gradients and to move into the open if sunshine provides opportunity for them to bask. Extent of tolerance to low temperatures was demonstrated on January 4, 1959, when air temperature was down to —12°. Although an oil heater was burning in the laboratory building, the temperature inside was below freezing. A group of copperheads being kept in the building, in screen cages and glass jars, were all immobile and lifeless in appearance and had temperatures somewhat below 0° C. Some that were nearest a window were frozen solid, but most were limp. Although at first assumed to be dead, more than a dozen of these snakes survived after subsequent slow warming. About the same number, including all those that were frozen solid, failed to revive. On January 17 and 20 experiments were performed with the survivors by removing them from the artificially heated room to subfreezing outdoor temperatures. The snakes placed outside continued to move about in their containers as the temperature dropped, and were still moving at 0° C. or even —.5° but they became increasingly slow and stiff as temperature declined, and soon were completely immobilized. Such a snake could be handled with impunity and was completely limp and lifeless in appearance and effectively anesthetized. One that was cooled to —1.5° C. and then warmed, showed the first signs of life at 6° and it recovered completely. Several others that were cooled to —1.5° and some of those that were cooled to —1° failed to revive. It seems that these temperatures are near the critical minimum. For reasons that are not evident individuals seem to differ notably in their capacity to withstand low temperature. At approximately —1.0° to —1.5° body fluids began to congeal, with release of heat, and even at air temperatures several degrees below freezing the decline in body temperature tended to pause at this level for periods up to a half hour. One juvenile that was kept for over an hour at a body temperature of —1° was somewhat stiffened by partial congealing of body fluids, but it revived completely. While it was being revived frequent stimulation was applied to test its reactions. For many minutes it was completely limp and inert showing no responses to pinches

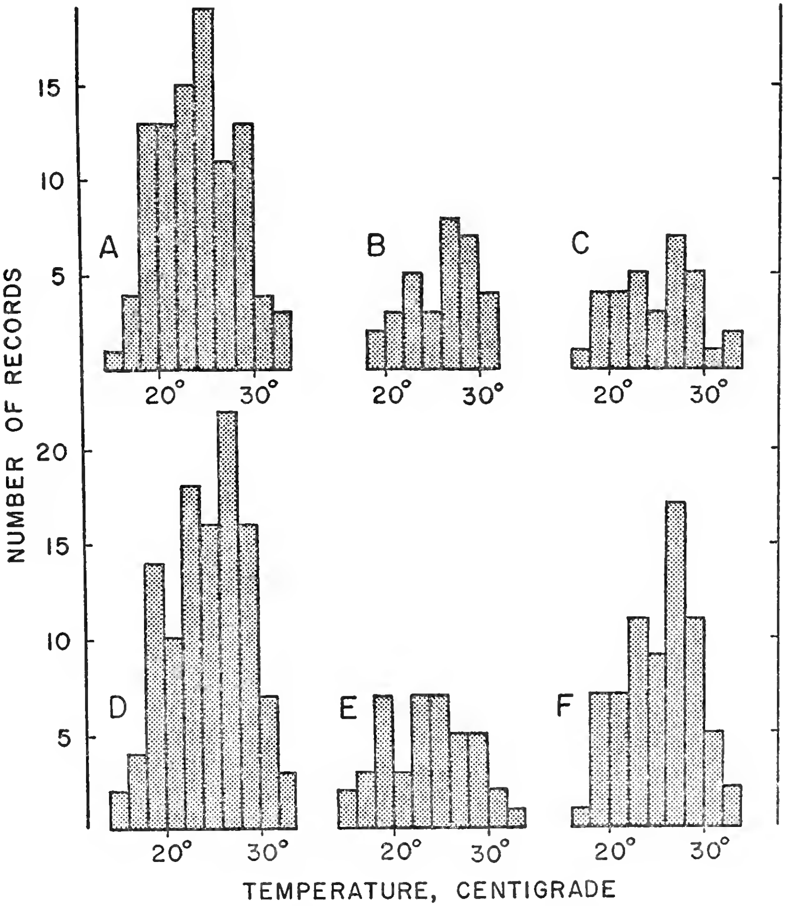

FIG. 14. Records of temperatures (in degrees Centigrade) at captures of copperheads in eastern Kansas (Douglas Co., with a few from Anderson, Jefferson, Linn and Miami counties). A. Temperatures of air at times and places where captures were made. The largest number of snakes was found at air temperatures between 24° and 26°. B. Bodily temperatures in gravid females found in the open. In the gestation period the females often bask and they tend to maintain relatively high temperatures. C. Bodily temperatures of non-gravid individuals (both sexes) found in the open. D. Bodily temperatures of copperheads found under natural conditions, including both those found in the open and those found under shelter. Favorite temperatures seem to be between 26° and 28°. E. Bodily temperatures of copperheads found under shelter. F. Bodily temperatures of copperheads found in the open; presumably these active snakes were regulating their temperatures to some extent by behavior, and their preferences for the range 26° to 28° is more evident than in those found under shelter.

or pricks until its temperature had risen to 13.9°. Then it moved slightly. First breathing occurred at 19.9°, and soon thereafter the snake had revived completely.

Bodily temperatures were obtained from 112 copperheads found under natural conditions in the course of my study; 70 were in the open and 42 were under cover. Presumably most snakes of both groups were exercising some control over their bodily temperatures by their behavioral responses to environmental temperatures. However, some of those found under rocks were cold and stiff and were obviously incapable of exerting any control over their temperatures, which were those of the surrounding soil and rock. The snakes that were in the open regulated their temperatures to a large extent by their movements between shade and sunshine, and by maintaining contact with objects in the environment having temperatures nearest their preferred levels. Therefore, these snakes that were found in the open fell within a slightly narrower temperature range than those under cover and they were more concentrated near the temperature that probably represents the optimum level (Fig. 14). The preferred temperature level seems to be between 26° and 28°, as previously concluded (Fitch, 1956:464).

Temperatures were measured with a Schultheis thermometer inserted into the cloaca. In the elongate body of a snake different parts of the body probably differ notably in their temperatures. In one copperhead found basking beside a crevice with part of its body exposed to sunshine on May 5, 1958, at an air temperature of 19.5°, the oral temperature was 30.5° while the cloacal temperature was only 24.8°. Differences of similar magnitude probably occur frequently in individuals that are active. In those exposed to sunshine the head and forebody tend to be warmer. The posterior end of the body and the tail sometimes remain in shade even when the snake seeks sunshine to warm itself, or at least their exposure to sunshine is delayed as the snake moves slowly into the open. All but one of the snakes having temperatures of less than 18° were found under rocks. Some of the lowest temperatures (17.0°, 16.4°, 15.5°, 14.0°, 13.7°, 12.4°) were recorded in early spring in copperheads found under large flat rocks; these individuals probably had not yet ventured into the open but were still in the process of emerging from their hibernation shelters.

Gravid females probably prefer temperatures somewhat higher than those preferred by other individuals; at least most of the copperheads found basking in sunshine in summer were females.

In September, 1958, a gravid female, a yearling, and four adult males were kept together in an outdoor enclosure of 100 square feet. From time to time bodily temperatures of all snakes in this group were recorded within a few minutes. Eight sets of readings are shown in Table 3. In six instances the gravid female had the highest reading of the entire group and her average exceeded the average of the group by 2.2° C. The yearling also tended to be warmer than the adult males; under the conditions of the experiment, with temperature of the air somewhat below optimum level, this small snake's ability to warm himself more rapidly by basking gave him a distinct advantage over the larger individuals.

TABLE 3. BODILY TEMPERATURES, IN DEGREES CENTIGRADE, OF A GROUP OF COPPERHEADS IN AN OUTDOOR ENCLOSURE

DATE AND TIME	Temperatures of individuals					
	Gravid female	Year-ling	Male No.1	Male No. 2	Male No. 3	Male No. 4
September 16, 1:50 P. M.....	21.8	24.8	22.5	21.3	20.6	22.0
September 17, 2:00 P. M.....	26.8	23.5	23.3	23.9	21.9	26.0
September 18, 11:30 A. M.....	28.3	26.0	22.8	22.0	21.3	22.7
September 18, 2:30 P. M.....	25.7	25.6	23.8	24.3	22.4	26.0
September 18, 4:45 P. M.....	30.4	25.7	24.6	24.6	23.7	24.7
September 21, 10:15 A. M.....	15.8	15.0	15.3	15.3	15.0	15.0
September 21, 1:10 P. M.....	21.7	19.8	18.2	19.7	16.2	19.3
September 21, 3:20 P. M.....	24.6	22.7	19.4	20.3	19.6	23.5

MOVEMENTS

No individual copperhead was recaptured a sufficient number of times to demonstrate the extent of its home range, but there is good evidence that home ranges do exist. Otherwise a copperhead would tend to wander gradually farther from its birth place. Several copperheads were recaptured as adults near the locations where they were born, and the great majority of recapture records were within, at most, a few hundred feet of the place where the same snake had been caught before, even though in many instances, years had elapsed since the original capture. Attachment to a familiar area satisfying all the essentials for existence seems to be characteristic of this species as it is of most kinds of terrestrial vertebrates. Nevertheless there are occasional shifts to new areas.

Three distinct types of movements can be recognized in the copperhead: (1) Travel within the home range; the movements of an individual in the course of its routine activities. Almost all the movements are of this type. (2) Shifts that involve abandonment of an original home range and occupancy of a new one. These movements are relatively rare but ecologically significant. Some individuals may live their entire lives within the same home range. Others may shift several times. As compared with females, males seem to shift more frequently and farther. (3) Seasonal migration between a hibernaculum, usually at a hilltop rock ledge, and a home range that is occupied during the summer. Some individuals, especially first-year young and gravid females, tend to remain on rocky slopes throughout the summer, and hence have home ranges that encompass their hibernacula. Other individuals make trips of hundreds of yards, if not farther, between their home ranges and their hibernacula. The place used for hibernation and the route leading to it might be regarded as an extension of the home range; however the hibernaculum may be relatively remote from the summer range and separated from it by areas of less favorable habitat, which the snake crosses in a fairly direct route.

In an earlier discussion of home range in the copperhead (Fitch, 1958:125), based upon much less extensive data, especially for movements on the summer range, I failed to distinguish clearly between the three types of movements. In actual practice it is impossible to distinguish between the three types in all instances. Data concerning size of home range were obtained chiefly in 1957, 1958 and 1959; few traps were operated in the summers of earlier years. For most individuals only two records are available, separated by a substantial interval. Therefore no home range can be plotted, but the distance between successive points of capture shows in a general way the size of the home range. Assuming that each snake wanders more or less at random within its home range (as copperheads seem to do), any two points of capture for the same individual would be separated *on the average* by a distance equivalent to approximately half the diameter of the home range. Since home ranges tend toward a circular shape except when distorted by peculiarities of the terrain or habitat, the formula πr^2 for the area of a circle should apply (Fitch, *op. cit.*:73). Doubtless home ranges vary greatly in size and shape, but the measured movements of a sufficiently large number of individuals should indicate the size of an average home range. Table 4 shows a series of movements of 26 individuals that are thought to represent normal movements within a home range in each instance. In these sets of records elapsed time varies from two weeks to nearly five years.

TABLE 4. DISTANCES BETWEEN SUCCESSIVE CAPTURES OF INDIVIDUAL COPPERHEADS ON THEIR SUMMER RANGES

INTERVALS BETWEEN CAPTURES	Snout-vent length of snake (mm.)	Distance between points of capture (feet)
Males		
June 30, 1958 to August 4, 1959	383	1240
June 2, 1958 to July 17, 1958	498	1150
August 13, 1959 to September 22, 1959	560	900
August 5, 1950 to May 20, 1952	578	720
August 19, 1950 to May 3, 1955	617	650
July 14, 1958 to July 12, 1959	778	550
May 16, 1958 to July 25, 1958	726	520
June 12, 1959 to August 4, 1959	445	360
July 14, 1956 to July 3, 1958	623	170
May 27, 1958 to July 22, 1958	920	150
Females		
June 5, 1958 to August 28, 1959	614	1000
July 6, 1954 to June 3, 1958	595	950
June 11, 1957 to July 22, 1958	556	950
June 27, 1955 to June 16, 1958	505	500
May 18, 1954 to July 3, 1958	667	410
June 30, 1958 to August 18, 1958	655	380
June 5, 1958 to May 29, 1959	511	250
May 28, 1958 to June 1, 1958	680	210
June 11, 1957 to June 14, 1958	550	150
June 27, 1951 to July 17, 1951	593	120
August 3, 1951 to August 27, 1951	593	120
July 31, 1949 to August 28, 1950	443	90
July 4, 1958 to July 15, 1958	406	40
July 17, 1951 to August 3, 1951	593	10
August 27, 1951 to August 6, 1953	593	5

The distances recorded in Table 4 are rather evenly distributed from zero up to 1240 feet, as might be expected if all are within home ranges. The averages are 581 feet for males indicating a home range having a diameter of 1162 feet and an area of 24.4 acres, and 345 feet for females indicating a home range having a diameter of 690 feet and an area of 8.5 acres. That some of the distances between captures exceed the 1162 feet computed to be the average diameter for males and the 690 feet computed to be the average diameter for females may be explained by the fact that some of the ranges are considerably larger than the average, and that some are of elongate shape—shorter than 1162 feet (or 690 feet) in one direction and longer in the other. The upper limits have been set arbitrarily, and several relatively long movements have been excluded on the assumption that they probably represent shifts from one home range to another. These movements are shown in Table 5.

Whether these exceptionally long movements differ merely in degree or differ in kind from the movements listed in Table 4 can not be proven with the information now available. Some individuals probably have home ranges that are much larger than the average, or are elongate and irregular in shape, or are composed of disjunct segments. It is doubtful whether the home range of a copperhead comprises a sharply defined entity. Insofar as is known, an individual snake has no central "home" to which it returns regularly for shelter, or any other purpose. Rather, it seems to wander about in a circuitous and irregular course. In view of the snake's sluggish habits and slow rate of travel, the home range seems remarkably large, and a long time would be required (many days, I should think) for the snake to cover the home range or even to travel across it. It is not evident whether precise boundaries exist, and what factors normally prevent the snake from wandering beyond the limits of the home range.

TABLE 5. DISTANCES BETWEEN POINTS OF CAPTURE IN SUMMER, OF COPPERHEADS EACH THOUGHT TO HAVE SHIFTED FROM ONE HOME RANGE TO ANOTHER BECAUSE OF THE RELATIVELY LONG TRIPS INVOLVED

INTERVALS BETWEEN CAPTURES	Snout-vent length of snake (mm.)	Distance between points of capture (feet)
Males		
June 12, 1959 to July 18, 1959	395	2500
June 25, 1959 to September 22, 1959	448	2350
July 28, 1958 to August 4, 1959	600	2140
June 10, 1958 to July 20, 1958	563	1600
Female		
June 25, 1958 to August 9, 1959	484	1450

Ordinarily a copperhead's view of its surroundings is limited to a few inches because of its preferences for situations having dense vegetation. Distant landmarks on the horizon, which might serve for orientation, are therefore rarely in view, and, in any case, may be imperceptible to the snake because of the latter's nearsightedness. Seasonal changes in ground vegetation and other features of the microhabitat are so great that a spot might be scarcely recognizable after the several weeks that probably would elapse before the snake happened to return. Also, the snake does most of its travelling in darkness. Olfactory, auditory and tactile cues likewise seem inadequate to keep the snake oriented within its home range, but perhaps all of these are involved. Certainly location memory must be well developed.

Various authors, including Babcock (1929:26) in Massachusetts, Ditmars (1935:23) and Oliver (1955:174) in the New York region, McCauley (1945:131) in Maryland, and Swanson (1952:176) in Pennsylvania have mentioned the seasonal movements of copperheads between the rocky hilltop areas where they characteristically hibernate and the places, often in lowlands, where they spend the summer, but no statement has been made of the distances involved.

TABLE 6. DISTANCES BETWEEN SITES OF AUTUMN OR SPRING CAPTURES AT HILLTOP LEDGES WHERE HIBERNATION OCCURS AND SUMMER CAPTURES ELSEWHERE, FOR INDIVIDUAL SNAKES, INDICATING POSSIBLE EXTENT OF SEASONAL MIGRATION TO AND FROM HIBERNACULA

INTERVALS BETWEEN CAPTURES	Snout-vent length of snake (mm.)	Distance between points of capture (feet)
Males		
August 4, 1958 to April 26, 1959	513	3880
October 16, 1958 to August 15, 1959	533	3200
May 18, 1957 to June 30, 1958	409	2940
September 21, 1951 to August 28, 1952	691	2320
September 29, 1949 to May 5, 1952	385	2250
October 13, 1956 to May 10, 1958	790	2200
September 19, 1953 to July 27, 1955	728	1890
July 2, 1954 to October 5, 1954	421	1640
October 31, 1958 to October 25, 1959	492	1550
May 27, 1958 to October 12, 1959	920	1440
August 19, 1958 to October 8, 1958	590	1300
August 15, 1959 to September 7, 1959	575	1200
Females		
October 4, 1956 to July 12, 1957	548	2070
October 1, 1951 to May 28, 1952	584	1950
June 5, 1958 to October 20, 1959	433	1680
September 25, 1957 to July 28, 1958	457	1600
May 22, 1952 to November 5, 1952	580	1550
June 20, 1955 to November 1, 1955	519	1100
September 25, 1957 to July 28, 1958	457	1100
July 5, 1954 to September 9, 1957	700	1060
October 7, 1955 to May 16, 1958	537	990
October 14, 1958 to August 5, 1959	447	800
September 30, 1958 to June 13, 1959	408	760

Vernon Mann, in conversation April 29, 1958, told me that he thought copperheads made much shorter seasonal movements than did timber rattlesnakes, but might make trips up to a mile or two. This was merely an impression, based on Mann's extensive experience with copperheads in Linn and Miami counties, Kansas. On the basis of my own experience I would consider a migration as long as a mile to be highly exceptional. In my study the marked snakes captured both at a hibernation ledge, and at a location away from a ledge in summer, had moved the distances shown in Table 6. These distances are assumed to represent trips between hibernacula and summer ranges although in some instances the snake may have been caught while still travelling toward or away from the summer range, and in other instances by the time of the second capture the snake may have permanently abandoned an original home range or hibernaculum. The circumstance of whether the capture in the home range happened to be in the part nearest the hibernaculum or most remote from it had considerable influence on the figures.

For the 12 males in this group, distance averaged 2151 feet and for the 11 females 1333 feet, indicating that, on the average, males travel much the farther in their trips to and from hibernation shelters. Not included in this table are the records of 18 males and 18 females that made recorded movements of less than the computed diameter of a home range (1162 feet for males, 690 feet for females) and hence may have had their hibernacula within their summer ranges. The trend of available data suggests that nearly two-thirds of the snakes remain throughout the summer in a range that encompasses the rock ledge where the hibernaculum is situated, and that for the remaining snakes migrations averaging a quarter mile for females and nearly half a mile for males are made to and from the hibernacula.

Snakes that congregate in large numbers at communal hibernacula have been generally supposed to return to the same den year after year. Findings by Woodbury (1951:12) at a den in Tooele County, Utah, used by rattlesnakes (*Crotalus viridis lutosus*), bull snakes (*Pituophis catenifer deserticola*) and striped racers (*Masticophis taeniatus taeniatus*), bear out this supposition. Whether other snakes, which hibernate singly or in small groups, return consistently to the same locations has not been satisfactorily demonstrated. However, the marked copperheads that I recaptured demonstrated notable fidelity to the stretches of ledge where they had been originally captured.

A male, first caught when he was of four-year-old size on October 10, 1949, was recaptured along the same hilltop rock ledge on April 26, 1952, October 1, 1955, and May 14, 1957; all four captures within 210 feet of each other. His only other capture was made on May 18, 1952, at the head of a valley at the base of the hill where the ledge was located, 1000 feet from the nearest part of the ledge, and he presumably was either on his summer range or travelling toward it. Another male first caught on September 17, 1951, when he was of four-year-old size, was recaptured 205 feet farther along the same ledge on October 22, 1954, and on October 20, 1958, he was within 30 feet of the second location. A male of two-year-old size on November 12, 1954, was recaptured October 13, 1956, and October 31, 1957, within a 350-foot stretch of ledge. An old adult female was captured on the same ledge on October 15, 1957, November 15, 1958, and October 17, 1959. The second capture was 355 feet from the first, but the third capture was made at the original location. Another female of three-year-old size when first captured on September 9, 1949, was recaptured 465 feet along the ledge on August 24, 1951, and on October 2, 1955, a third capture was made 110 feet from the second, in the direction of the first. A female of five-year-old size when first captured at a ledge on September 30, 1950, was recaptured at the same place on November 9, 1954; on August 12, 1952, she was found at another place on the ledge 110 feet from the site of the first and third captures.

The snakes caught along the ledges in autumn and spring were not necessarily in the vicinity of their hibernacula, as some spend several weeks at a ledge in autumn before hibernating and may travel for varying distances along the outcrop in the interval. Hence it is not surprising that individuals were often found hundreds of feet along the ledge from a previous capture site. It is not definitely proven that an individual returns year after year to the same rock crevice to hibernate, but the fact that some individuals had returned to the same spots on the ledge where they were captured in former years does suggest fidelity to a specific hibernaculum. For most individuals only two years' records of capture at the ledges are available. These records are shown in Table 7. Table 8 shows records of those individuals that were recaptured at different stretches of ledge, having moved many hundreds of feet from an original location, and perhaps shifted to an area altogether separate from the one originally occupied. The ratio of six males to two females in this series is noteworthy, and

TABLE 7. DISTANCES BETWEEN CAPTURE POINTS OF COPPERHEADS EACH OF WHICH WAS CAUGHT AT A HIBERNATION LEDGE IN TWO DIFFERENT YEARS

INTERVALS BETWEEN CAPTURES	Snout-vent length of snake (mm.)	Distance between points of capture (feet)
Males		
April 19, to September 30, 1958	508	600
October 5, 1949 to September 19, 1950	456	500
September 27, 1958 to October 27, 1959	686	460
September 27, 1957 to September 20, 1958	623	435
October 10, 1958 to October 6, 1959	420	425
October 5, 1957 to September 24, 1958	544	400
September 17, 1955 to September 27, 1957	678	370
October 13, 1956 to October 31, 1957	628	350
October 5, 1957 to September 24, 1958	544	320
May 5, 1950 to October 17, 1950	633	300
October 5, 1949 to August 30, 1952	630	270
September 3, 1949 to October 2, 1951	344	260
October 14, 1955 to October 13, 1956	655	250
October 24, 1951 to October 24, 1957	765	235
April 26, 1952 to October 1, 1955	820	210
November 12, 1954 to October 13, 1956	427	205
October 1, 1955 to May 14, 1957	890	200
September 29, 1949 to September 26, 1951	458	150
October 23, 1953 to October 10, 1955	390	150
September 3, 1949 to September 28, 1950	348	100
September 17, 1952 to September 18, 1957	785	100
October 2, 1953 to October 17, 1954	474	100
October 17, 1954 to October 16, 1956	593	90
October 24, 1957 to September 24, 1958	603	90
October 11, 1949 to April 26, 1952	663	80
April 19, 1958 to October 11, 1958	560	60
October 13, 1954 to October 2, 1955	378	40
October 22, 1954 to October 20, 1958	764	30
October 24, 1957 to November 15, 1958	553	30
October 5, 1954 to October 7, 1958	765	25
September 17, 1958 to October 8, 1959	423	20
October 16, 1956 to October 11, 1958	378	10
October 17, 1950 to October 20, 1951	674	same location
Females		
May 12, 1952 to October 22, 1952	628	655
October 10, 1950 to October 4, 1953	337	600
September 14, 1951 to October 17, 1953	548	560
September 9, 1949 to August 24, 1951	525	465
October 15, 1957 to November 15, 1958	670	425
November 15, 1958 to October 17, 1959	670	425
September 17, 1958 to September 26, 1959	525	350
September 13, 1949 to April 24, 1951	373	350
April 15, 1950 to August 5, 1950	618	300
October 24, 1951 to October 20, 1953	333	270
October 15, 1957 to November 15, 1958	670	200
October 3, 1949 to October 15, 1951	432	170
October 4, 1951 to September 9, 1955	442	170
September 29, 1949 to September 26, 1951	458	150
August 24, 1951 to October 21, 1955	616	110
November 11, 1955 to October 10, 1958	535	100

TABLE 7. DISTANCES BETWEEN CAPTURE POINTS OF COPPERHEADS EACH OF WHICH WAS CAUGHT AT A HIBERNATION LEDGE IN TWO DIFFERENT YEARS—*Concluded*

INTERVALS BETWEEN CAPTURES	Snout-vent length of snake (mm.)	Distance between points of capture (feet)
September 17, 1957 to September 1, 1958......	590	70
September 30, 1950 to November 9, 1954......	574	25
October 15, 1952 to September 19, 1953........	589	10
October 28, 1955 to September 5, 1956........	388	same location
September 30, 1950 to November 9, 1954......	574	same location

bears out other data indicating that females are less vagile than males.

Table 8 shows the records of individuals that returned at least to the same vicinity along the ledge. Probably most of them dispersed to other areas each summer. For the majority this is not definitely known, but some were actually captured on their summer ranges, and these records form, in part, the basis for Table 5.

Because of inefficient techniques of collecting, relatively few of the snakes present in the area of operations could be caught in one year. Therefore, most individuals were caught only once and for most of the remaining snakes only two captures were recorded. However, for some of these, recaptures were made after lapses of

TABLE 8. DISTANCES BETWEEN CAPTURE POINTS OF COPPERHEADS EACH OF WHICH WAS CAUGHT AT DIFFERENT HIBERNATION LEDGES IN TWO DIFFERENT YEARS

INTERVALS BETWEEN CAPTURES	Snout-vent length of snake (mm.)	Distance between points of capture (feet)
Males		
September 29, 1949 to May 5, 1952...........	458	2250
October 31, 1958 to October 25, 1959..........	492	1550
October 3, 1950 to October 2, 1951............	647	1300
September 23, 1952 to September 5, 1953......	637	1200
September 16, 1954 to October 4, 1957........	630	1160
September 2, 1950 to September 24, 1958......	351	960
Females		
October 1, 1951 to September 29, 1954........	584	1760
April 20, 1955 to October 8, 1955.............	558	1380

TABLE 9. DISPERSAL OF YOUNG COPPERHEADS THAT WERE EITHER BORN IN CAPTIVITY AND RELEASED AT CAPTURE POINT OF MOTHER OR THAT WERE CAPTURED SOON BEFORE OR AFTER THE FIRST HIBERNATION AND WERE RECAPTURED AFTER SUBSTANTIAL INTERVALS. ALL WERE IN THE LENGTH RANGE 187 MM. TO 282 MM. WHEN THEY WERE MARKED

DATES OF RELEASE AND RECAPTURE	Snout-vent length at recapture (mm.)	Distance between points of capture (feet)
Males		
September 11, 1954 to May 14, 1957	460	3100
June 1, 1953 to October 16, 1957	571	3050
October 15, 1951 to September 29, 1954	517	2340
August 28, 1952 to August 19, 1958	691	2340
September 5, 1954 to October 6, 1956	535	1900
September 6, 1954 to June 30, 1958	565	1560
September 9, 1952 to September 25, 1956	740	1440
May 2, 1953 to July 4, 1958	703	1240
September 5, 1954 to July 30, 1957	538	1120
September 1, 1951 to June 1, 1957	433	1100
October 8, 1954 to October 24, 1957	563	1100
September 6, 1954 to October 11, 1958	680	1020
November 8, 1954 to October 24, 1957	563	1000
September 4, 1954 to September 9, 1958	627	950
October 17, 1951 to June 11, 1955	510	920
October 17, 1951 to June 1, 1955	510	850
August 20, 1950 to May 28, 1952	347	720
September 19, 1953 to July 21, 1955	477	600
September 26, 1953 to September 23, 1955	465	600
September 1, 1954 to May 6, 1954	474	360
October 21, 1955 to October 9, 1957	495	200
May 21, 1953 to August 28, 1953	363	200
September 28, 1950 to September 31, 1951	303	160
September 28, 1950 to September 13, 1951	303	100
November 7, 1954 to October 5, 1955	439	70
September 5, 1952 to November 11, 1954	393	40
Females		
September 6, 1952 to November 1, 1957	622	3360
September 6, 1952 to June 1, 1958	606	2000
September 28, 1950 to August 31, 1955	582	1800
October 23, 1954 to July 8, 1958	544	1650
September 19, 1953 to June 4, 1958	536	1540
September 19, 1953 to June 5, 1957	558	1120
September 29, 1950 to November 2, 1958	644	1020
September 13, 1954 to September 29, 1955	403	960
September 29, 1955 to June 25, 1958	484	600
September 29, 1950 to November 2, 1958	644	500
August 20, 1950 to September 26, 1951	341	450
September 1, 1954 to April 27, 1957	502	385
September 11, 1954 to June 25, 1958	530	260
September 6, 1952 to June 2, 1955	495	90
June 4, 1953 to September 24, 1958	580	25

several years; after periods as long as six years the snake might be found again in the same neighborhood. Table 7 shows the following intervals: 28 snakes were recaptured after one year, 14 after two years, four after three years, seven after four years and one each after five and six years. Many other copperheads were caught two or more times along a ledge in the course of an autumn's trapping, or were caught in autumn and again in spring—soon before retiring into hibernation and soon after emerging. For such snakes, the distances between successive captures tended to be shorter than in the snakes whose captures spanned longer intervals. For males the distances (in feet) involved were: 590, 270, 165, 160, 130, 100, 100, 90, 90, 90, 90, 70, 70, 70, 60, 60, 50, 30, 30, 20, 10, 10, and for females: 440, 300, 190, 175, 163, 140, 100, 80, 60, 10.

Not included up to this point in the discussion or in the tables are the records of numerous young born in captivity or captured in autumn soon after birth, or in spring soon after emergence from their first hibernation, and recaptured after one or more seasons. The records of these individuals are assembled in Table 9. In general they are notable for the relatively long distances involved, as compared with the movements of other copperheads. Several exceed half a mile, probably indicating that young copperheads most often wander away from the immediate neighborhood of their birthplaces and become established in new areas. On the other hand some individuals were recaptured after periods of years in the neighborhoods of their birthplaces. In these snakes as in other groups of copperheads, the females are distinctly the more sedentary. Of the 26 males, 35 per cent had travelled less than 600 feet; of the 15 females 47 per cent had travelled less than this distance.

REPRODUCTION

Courtship and Mating

Sexual behavior has rarely been observed in the copperhead, probably because it normally occurs at night or under cover. Hay (1893:386) recorded a pair found mating on August 28. Knowing that young are born in late summer or early autumn, he erroneously concluded that the gestation period is nearly a year. Beyer (1898: 19) recorded a pair found mating on April 12, 1895, in Louisiana. He kept these snakes in captivity, and the female produced a litter of young on September 16. Guidry (1953:55) kept a female found in the act of copulation on May 3, 1952, in southeastern Texas, and she gave birth to a litter on August 21. Finneran (1948:124) found a mating pair on April 26, 1941, in Connecticut. Vernon Mann told me that he had often seen mating pairs along rock ledges in spring when the snakes had recently emerged from hibernation, and he considered this time to be the breeding season. Gloyd (1934:588) did not observe actual mating, but he concluded that the breeding season in eastern Kansas was in April and early May, a five- or six-weeks period after emergence from hibernation. He frequently found males and females together under the same rock in this period. Twenty-one of 59 sexually mature females that Gloyd obtained in April and May were found to have active sperm in their genital tracts.

On the Reservation, in the course of my study, pairs or groups including members of both sexes were found together on various occasions, in spring soon after emergence from hibernation. On April 6, 1959, a male and three females were found at a den entrance, and probably were newly emerged on that date, as none had been found earlier, and weather had been unfavorably cool most of the time. The male and one of the females had active sperm in their cloacae, evidence of recent mating.

Although copulation may be especially frequent at this time in spring when the snakes are concentrated along the ledges where they hibernate, there is no true breeding season. Gloyd (*loc. cit.*) examined *vasa deferentia* of freshly killed males in April, May, June, July, August and October, and all showed more or less active spermatozoa. A factor little understood until recent years is that of sperm storage in the female, and delayed fertilization, now known to occur in various reptiles, including a lizard (chameleon), turtles, and snakes of several different families (Fox, 1956:521). Production of fertile clutches after intervals of isolation as long as six years in the night snake, *Leptodeira annulata polysticta* (Haines, 1940: 116) and four years in the indigo snake, *Drymarchon corais couperi* (Carson, 1945:223) are known, although these records are exceptional. Allen (1955:228) presented conclusive evidence that the sperm may remain viable in the female copperhead for more than a year after copulation. An adult female from Texas (*A. c. laticinctus*) was received at the Highland Park Zoo in Pittsburgh in July, 1954. On August 24 of that year she gave birth to a litter of five young, and again on August 20, 1955, she gave birth to a litter of five. "Since arrival at the Zoo she has shared her cage with no other snakes . . . had no contact with any males."

Fox (*loc. cit.*) studied the histology of the organs involved in sperm storage of snakes, and found that the anterior part of the oviduct is thick and convoluted, with many highly modified alveolar glands which serve as seminal receptacles. Clumps of sperm were often found tightly packed in these receptacles. Carson (*loc. cit.*) speculated that in sluggish kinds of snakes, living in low population densities, powers of sexual search may be inadequate to assure fertilization, so that prolonged sperm viability would have definite survival value. The copperhead would seem to be benefited by prolonged sperm viability, especially where it exists in sparse populations.

In 1959 I tested many individuals of both sexes for active sperm. A few were sacrificed for dissection, but most were released unharmed after collection of cloacal fluid. The cloaca was cleared of fecal material and uric acid by gentle massaging, and a small vial of Ringer's Solution was emptied into it. After further massaging (to express sperm from the *vas deferens*) the fluid was withdrawn into the vial. Nearly all adult males tested were found to have active sperm, and the sample included individuals collected in every month throughout the season of activity. Evidently adult males are continually in breeding condition. Relatively few of the females collected at any time of year were positive in these tests. Sperm probably persist for a relatively short time in the cloaca, but survive much longer in the upper end of the oviduct, in vascular tissues specialized as seminal receptacles. Adult females positive for active sperm in the cloaca, were recorded on the following dates: April 6, April 27, May 19, May 20, June 1, October 20, October 25, and October 27. Others found to be negative for sperm were collected on April 6, April 21 (2), April 27 (3), June 12, July 12, July 23, July 24, July 29 (4), July 30, August 21, October 17, October 21, October 25, October 27, November 4 (3), November 7, November 8 (3).

For rattlesnakes, Klauber (1956:692) has recorded matings in almost every month of the season of activity and some matings in captivity even in the winter. He concluded that in the southern United States rattlesnakes normally mate in spring, soon after they come out of their winter retreats but that farther north, where biennial broods are the rule, the mating times may be more widely dispersed and summer or fall matings may even predominate.

In the copperhead it is my impression that mating may occur almost any time in the snakes' season of activity, especially when the snakes are concentrated along the hibernation ledges in spring and fall, but that there is some tendency for concentrated sexual activity a few weeks after the spring emergence, at about the time when the females are ovulating—the latter half of May.

On May 19, 1959, a pair was found in a trap. The female's cloaca contained semen swarming with active sperm—evidence of recent copulation. The female was kept isolated in confinement, and a second cloacal sample taken on June 24 was found to contain abundant motile sperm still. However, approximately three-fourths of the sperm in this sample were dead, and many others were notably slow in their movements.

In middle and late May, 1957, several males were introduced at different times into the cage of a female which had been reared to small adult size in captivity. In each instance the male was introduced near dark or shortly afterward and observations were made from time to time subsequently over periods of hours. Courtship, and probably copulation took place in each instance but the copperheads were remarkably sensitive to disturbance. When light was flashed onto the cage, activity was interrupted as the snakes "froze"; however their positions indicated that courtship had been underway. The male would be found following the female or extended along her, sometimes with his tail looped beneath hers. The first male introduced was a recaptured, marked young 32 months old. Although far short of adult size, he was sexually mature. At dusk, within a few minutes after being introduced into the cage, he evinced interest in the female, flicking her with his tongue, and then following beside her or over her as she moved. The female's behavior indicated some stimulation by this courtship. Her movements became more animated and jerky than usual, with apparent nervousness. She tended to react to contact of the male by pushing him away. Convexities of her coils were used as pressure points, and with sudden, perhaps involuntary spasmodic contractions, she would "bump" the male forcing him aside a short distance, but she was not actively hostile.

It might be expected that sexual attraction and inclination to mate would be reflected in the trapping records in "double" captures involving an adult male and female in the same trap. Double or multiple captures were made from time to time throughout the season that traps were operated, especially in October when most copperheads were concentrated along the hibernation ledges, and seemed to trail each other to find suitable shelter. The combinations of individuals in traps usually indicated that sexual attraction was not the basis for the aggregations. However, in the latter half of May pairs were caught more often than at other times. In 1958, for example, eight of the 17 adults trapped from May 16 to 31 were in pairs. Presumably they had entered the traps together or else the males had trailed the females into the traps.

In several instances I found copperheads in pairs under circumstances suggestive of sexual activity in autumn. On the morning of September 26, 1951, a pair was found coiled together in dry leaves in thick woods of a southwest slope. For ten minutes that they were observed they remained motionless. The larger was then caught and was found to have his hemipenis partly everted. Pairs were caught in traps on September 25 and 27.

Munro (1950:88) described what seemed to be courtship behavior in a pair of copperheads said to be four years old and probably kept for a long time in captivity. When they were placed in the same cage they made bobbing head-movements each time they met in moving about the cage. The movements of the male were the more vigorous. After being kept together for several weeks they would still bob occasionally. During courtship (when the bobbing became "very agitated"), the tail and posterior parts of the body executed lateral wriggling and writhing movements not noticeably coordinated with the bobbing of the head.

Ian D. W. Sutherland has described (*in litt.*) courtship behavior in a pair of copperheads that were obtained in Kentucky in 1955 and kept in captivity for several years. The snakes were kept at a temperature averaging approximately 75° F. and did not hibernate. Courtship occurred irregularly over an eleven-month period in 1957 and 1958. From August to January the male evinced consistent interest in the same female. From January to June only infrequent courting occurred, and then with reduced excitation. On December 19, 1957, the female copperhead moved from one corner of the cage toward the center, and the male in another part of the cage exhibited immediate excitation. He moved toward her and came in contact with the posterior part of her body. The female's movements ceased when the male made contact. The male then became moderately excited and began to rub his chin along her body in short spasmodic jerks. At first he moved toward the posterior end of her body but corrected his direction and progressed anteriorly, rapidly protruding his tongue, with the points widely spread. When he reached the anterior end of the female, he placed the posterior part of his body alongside and forced it under the female with a rippling movement. When the female began to crawl, the male became extremely active and moved his entire body convulsively, causing the posterior part to disengage and thrash about wildly. The male's head was moved vigorously along the top of the female's head. The posterior portion of his body was again brought alongside the female's body and his tail was twisted encircling hers. The posterior portion of the male's body contracted longitudinally, and forced the female's tail up and forward. The male's head movements increased and his body was in continual movement alongside the body of the female. The female remained impassive during the entire period of courtship.

Fecundity of Females

The proportion of adult females that breed each year cannot be readily determined. Gravid and non-gravid females differ somewhat in habits. As a result, samples are liable to be biased. Gravid females tend to stay nearer the hilltop rock ledges than do males, and spend a relatively large amount of time in basking. In a seven-year sample of summer records, 1950 through 1956, there were 54 gravid females and only 12 that were not gravid. All but six of the total of 66 were found on or near hilltop ledges. In the summers of 1957, 1958 and 1959, when extensive trap lines were maintained, chiefly in open fields, a much different ratio was obtained: 29 gravid females and 46 that were non-gravid. In the combined ten-year sample there were 76 from ledges, including 68 gravid and 8 non-gravid, and there were 57 from fields, including 12 gravid and 45 non-gravid.

Probably the gravid females are represented by disproportionately high numbers in my sample because they are more easily found than those that are non-gravid being concentrated along the ledges and being more inclined to bask in the open. From the high proportion of females that are not gravid during the summer, it is obvious that a typical adult female does not produce a litter each year. It seems most plausible to suppose that litters are produced in alternate years, and this supposition is borne out by the breeding records of all individuals that were caught as adults in more than one summer. A female, gravid when caught on June 11, 1957, weighed 168 grams. She was recaptured on July 22, 1958, and was then not gravid, weighing only 133 grams. Another female caught on October 1, 1951, was emaciated (112 grams) having the appearance of recent parturition. Almost exactly three years later, on September 29, 1954, she was recaptured after the season's litters had been born; she had made substantial growth and was plump (222 grams) indicating that she had not produced a litter recently. Another female, gravid on July 5, 1954 (329 grams), was recaptured on September 7, 1957, and was not then gravid (247 grams) nor did she appear to have given birth to a litter recently. Five other female copperheads were captured when gravid and were recaptured after two-year intervals when again gravid. Two others that were captured when gravid were recaptured again gravid after intervals of four years. In summary, of ten females originally recorded as gravid, three were not gravid when recaptured in odd numbered years, and seven were again gravid when recaptured in even numbered years; although this sample is small, it indicates rather convincingly that in the region of my study females ordinarily produce their litters only in alternate years. That this pattern may not hold throughout the range of the species and particularly in the southern part is indicated by Allen's (*loc. cit.*) record of a female from Texas that produced successive litters on August 24, 1954, and August 20, 1955.

Since individuals grow at much different rates they may attain sexual maturity at different ages. At an age of three years most but not all are of small adult size and are sexually mature. Several of the young that were marked at birth were recaptured as young adults. One born on September 24, 1950, was recaptured on October 12 and November 9, 1954, and on the latter date it was dead in the trap. Although it had attained a size typical of individuals in their sixth year, its ovaries and oviducts were small and obviously it had not bred that year. Another female born on September 19, 1953, was recaptured on June 5, 1957, and then was of adult size (558 mm.) but seemingly not gravid (160 grams). A female born on October 24, 1954, was recaptured on July 8, 1958, and had grown to small adult size (544 mm.) but was definitely not gravid (130 grams). Another born on September 29, 1955, was recaptured on August 9, 1959, and was then definitely not gravid (122 grams). Another born in captivity on September 9, 1954, was recaptured late in her fifth year on June 30, 1959, and was tentatively recorded as gravid on that date. Another marked soon after birth on September 29, 1955, was recaptured when nearly four years old, on August 9, 1959, and she was then definitely not gravid. Still another female born on September 11, 1954, was recaptured on June 25, 1958, and appeared to be gravid. This female was kept throughout the summer, but did not produce a litter and by late August she no longer had the appearance of being gravid. Either the original diagnosis of pregnancy was erroneous or, possibly the ova were absorbed under the unfavorable conditions of captivity. Three individuals each were caught when approximately five years old; one born on September 28, 1950, was recaptured on August 31, 1955, in late pregnancy (length 582 mm., weight 196 g.). Another born on September 6, 1952, was recaptured on November 1, 1957, and had the characteristic thin and wrinkled appearance of those that have recently given birth to a litter (length 622 mm., weight 106 g.) A third born on September 19, 1953, was recaptured on June 4, 1958, and appeared to be in early pregnancy then (length 536 mm., weight 110 g.). Thus none of the six four-year-olds in my records was breeding, whereas all of the four five-year-olds were produced litters. A female born on September 6, 1952, was recaptured on June 1, 1958; she did not seem to be gravid (length 606 mm., weight 143 g.) and had probably given birth to a litter the preceding September when she was five years old. The only deviate from the general trend of all these records was a female born on August 28, 1952, recaptured as a typical two-year-old (476 mm., 68 g.) on October 5, 1954, and recaptured when seemingly gravid (605 mm., 205 g.) on July 5, 1958. Presumably this pregnancy was her second, and probably she had produced her first litter at an age of four years.

Although the foregoing records indicate a trend of 9 to 1 for litters born to five-year-olds versus first litters born to four-year-olds, the sample is perhaps too small to be given much weight.

Development of Ova and Embryos

At the time of emergence from hibernation females have only small whitish ova in their ovaries. In any one female these ova tend to fall into several size groups suggesting that they may be destined for successive broods, but there are always some of intermediate sizes. Ova of the largest size group are ordinarily more numerous than are the young born in a brood. In May the ova enlarge rapidly, and ovulation occurs in the latter part of the month, at approximately the time when copulation often occurs. By then the females' bodies are slightly distended posteriorly by the enlarged ova, causing them to have a gravid appearance.

Females dissected at various times contained ovarian eggs, as indicated in Table 10. For the smaller eggs the measurements given are only rough approximations in most instances. Also, many of the more minute ova probably were overlooked. Because the smallest females recorded as producing litters or as definitely gravid were somewhat more than 500 mm. in snout-vent length, several of the females included in the table almost certainly were sexually immature. Some of the larger individuals, including both of those taken in June, were not breeding (since females breed only in alternate years) and their ova would not have reached full size until the following year. In the female taken on May 11, 1957, the largest eggs were approaching mature size. Ovarian eggs that are much enlarged turn from white to yellow. A female caught on June 22, 1959, and dissected, contained oviducal eggs that must have been recently ovulated, since embryos were not yet discernible, but

TABLE 10. SIZES AND NUMBERS OF OVARIAN EGGS IN FEMALE COPPERHEADS

DATE	Snout-vent length of female (mm.)	Weight of female (grams)	Length of eggs in mm.	
			Left ovary	Right ovary
April 8, 1953	500	75	6 5 5 4 2 1	6.5 5 5 4 2.5 2 2 1
April 8, 1953	536	117	9 8 7 5 5 3	9 9 6 5 5
April 21, 1959	634	248	(largest of five, 14 mm.)	(largest of seven, 14 mm.)
April 21, 1959	595	129	(largest of three, 5 mm.)	5
May, 1958...	394	35	1 1 1 1	1 1 1 .5 .5 .5 .5 .5 .5 (plus seven more of less than 2.5 mm.)
May, 1958...	437	52	5 5 4 4 4 3 3 3 1 1 1 1	5 5 5 5 2 2 2 2 1 1 1 1
May, 1958...	541	64	6 6 6 3 2 2 2	6 6 6 6 3 3 2 2 2
May, 1958...	452	49	5 4 4 2.5 2.5 2.5	4 4 4 2 2 2 2
May 11, 1957	552	119	20 16.5 16 11 (and four much smaller)	20 15 14 (and three much smaller)
June 10, 1958	850	104	5.5 4 4 2.5 2 2	6 6 6 5 5 5 2 2 2
June 12, 1957	665	280	11.7 9 8.6 7.4 7.3 7.1 4.8 4.3 3 3 2.9 2.3 2 2 1.3	9.1 8.8 8.8 8 7.9 4.2 3.8 3.5 1.9 1.9
July 12, 1959	622	145	(6 ova, 2–6 mm.)	(7 ova, 2–6 mm.)
Nov. 10, 1954	575	146	9 9 9 8 7 6 4 3 3 3	10 10 10 8.5 8 5 4.5 4.5 3 3 2

probably most individuals ovulate at least three weeks earlier, in late May.

After ovulation the eggs are elliptical, pale yellow, approximately twice as long as broad (average 34 x 17 mm. in eight clutches in preserved specimens). The embryos grow slowly, and after several weeks have assumed the elongate serpentine form, coiled within the egg. At first the head is relatively large, and the protruding eyes are conspicuous because of their dark pigment. Otherwise, the embryo is whitish and translucent. As development proceeds, the total volume of the egg increases; growth of the embryo and increase in the amount of amniotic fluid more than compensate for the yolk substance used up.

It is estimated that the gestation period—time from ovulation and fertilization of the egg to parturition—is typically in the neighborhood of 105-110 days, including the last week of May, the first week of September, and the entire months of June, July and August. Guidry's (*loc. cit.*) record of a 108-day period (May 3 to August 19) between copulation and parturition in southeastern Texas, probably represents a gestation period. As in other ectothermic animals, the gestation period in the copperhead probably is variable, being influenced to some extent by external conditions, especially temperature. Certainly conception does not necessarily occur soon after copulation, as it does in most mammals. Precise measurement of a gestation period is impossible because the time of ovulation and conception cannot be determined without sacrificing the individual.

Aggregating of Gravid Females

A characteristic habit of pregnant female copperheads is that of gathering in small aggregations. An early account of this habit was published by Allen (1868:179) from the observations of a Mr. A. C. Bennett in Massachusetts: "Of five specimens killed July 4th . . . all were females. . . . *They were all found in a heap.* At another time, later in July, seven were killed, which like the others, were all found lying within the space of a square yard and all were females. Five of them were examined by Mr. Bennett, and found to contain slightly developed embryos. . . . In September . . . six specimens, all females, and all found in a heap, were killed, each of which had either seven or nine young." Gloyd (1934:592) stated that ". . . on three occasions two or three gravid females were discovered in the same location. In 1927 two were in the crevice described [a pocketlike recess extending about a foot beneath a massive limestone slab, and having an opening about two inches high]; in 1928 there were three; in 1927 two others were sheltered by a flat stone four feet across." Finneran (1948:124 and 1953:61) described a den location at Branford, Connecticut, where each year from 1940 to 1947, he found aggregations of gravid females in late summer. The den was at the summit of a hill, with a rock ledge and loose rocks, in woodland with cedar, pine, laurel, and blueberry. Each year groups of five to 11 females were found, either in actual contact or at least in a small area. On July 31, 1941, five were found and on August 1, four more. In 1942 groups of seven to nine were found. In 1946 the area of aggregation was shifted about ten feet to a partially shaded site, where on September 7, nine gravid females were found. Four were found in 1947. Newborn young were found at this same site in September of several years, and seemingly the place was occupied by copperheads throughout the season of their activity.

Minton (1944:474) mentioned the gregarious tendencies of the copperhead, and stated "In addition to hibernating groups copperheads are frequently found in pairs or threes during the summer."

Aggregations of gravid females have been found on the Reservation on only three occasions. This may be attributed to their relatively low population density on the Reservation as contrasted with the areas where some other workers have observed them, and also to the fact that suitable cover is extraordinarily abundant. On August 3, 1950, late in the afternoon, in a rocky area near the summit of a south-facing slope, I turned a flat rock approximately two feet in diameter and two to three inches thick. The rock's lower edge was deeply embedded in the soil and its surface was inclined at approximately a 30-degree angle, with the upper edge clear of the substrate. Two large adult female copperheads were coiled together beneath it in a nestlike depression. Slightly moist soil lining the cavity was packed and smooth probably indicating occupancy of the cavity, at least over a period of several days. When the rock was raised, the snakes uncoiled and began moving away; one temporarily found shelter beneath the edge of the rock and the other moved off into high grass. Several minutes were required to capture and bag both the females. When this had been accomplished I heard the sound of a third snake gliding through the grass approaching the rock and the nest cavity. It was captured and was found to be another gravid female.

On August 8, 1950, a second aggregation was found 100 yards from the first, under a flat rock five feet from the ledge itself, which was overgrown with a thicket of skunkbrush, hackberry, hazel, and dogwood. The rock was in an open place in low grass and weeds and was approximately 26 by 18 by 3 inches. Four gravid female copperheads were beneath the rock, all in resting coils, in contact with each other. When uncovered they lay still at first, and I retreated to find a stick with which to pin down and catch them. As I approached again all four snakes were becoming restive, looking about alertly and beginning to move. They were not inclined to leave the depression under the rock, but were running their snouts slowly over the ground, seemingly searching for concealment. I caught three but meanwhile the fourth escaped over the edge of the ledge into thick brush. On the following day, a gravid female, probably the one that had escaped, was found coiled partly in sunshine on the sticks of an old wood rat house beneath a clump of skunkbrush at the ledge a few yards from the rock where the aggregation had been. The rock that sheltered this aggregation was exposed to sunshine from morning till late afternoon. On August 12, 1952, two gravid females were found coiled near together beneath a board at the old quarry site.

In contrast to these few instances when gravid females were found associated with each other on the Reservation, dozens of other gravid females were found or trapped alone. Even though there is some tendency to aggregate, the majority of individuals must remain solitary for most of the time. In the summers of 1957 and 1958 several gravid females and other copperheads were kept together in an outdoor enclosure of approximately 100 square feet. The females sometimes aggregated, but at other times rested separately, and occasionally were associated with males or juveniles.

Such social aggregations of gravid females seem to be almost unknown in other kinds of snakes. An indication of similar aggregations in another crotalid, the prairie rattlesnake, is provided by the field notes of A. M. Jackley, in South Dakota, quoted by Klauber (1956:695). ". . . late in August they find suitable holes or cavities wherein they give birth to their young. These places I call rookeries, since it is common to find a dozen or more females quite close together. The distances of the rookeries from the dens vary a good deal, but I think the majority are about half a mile from the dens, and rarely are they closer than 600 feet."

Time of Birth

Actual birth dates for copperheads of 123 litters recorded in my study or gleaned from the literature range from August 3 to November 6. But for any one locality and year the dates of normal parturition are far more concentrated than these dates indicate;

probably most of them fall within a two-week interval. Most birth dates are based upon females kept in captivity for varying intervals, and for those kept for several weeks the birth of litters may be delayed.

Unnatural prolonging of gestation in captivity was strikingly demonstrated in 1950 and 1951, when I kept many females, captured in July and August in order to obtain their litters. These females were maintained in the laboratory singly or in twos and threes, in small cages, and frequently were offered mice as food. The mice were usually soon struck and killed, but most often were left uneaten. Some of the snakes never fed and none ate normal amounts. As a result all were somewhat undernourished. Births of their litters were delayed, and averaged approximately a month later than the dates for other years.

The delayed parturition of undernourished females is regarded as an adaptive response through which some or all of the fetuses may be saved from destruction. Under natural conditions, in times of food scarcity, rate of development of the embryos would be slowed. Improved food supply late in pregnancy would permit some, at least, of the retarded embryos to complete their development. None of the undernourished females gave birth to a normal litter. Sometimes all the young were born dead, and stillbirths occurred in most of the litters. Even if born alive, the young were unusually small. The weight of some was as little as one-fourth of that of a normal newborn young. Despite their prolonged gestation such young seemed to be premature, not only in their small size, but in fetal head shape, bulging abdomens still distended with yolk, and skin incompletely cornified with underdeveloped scales. It is remarkable that several of these underdeveloped young born in captivity, marked and released, survived under natural conditions and were recaptured years later as adults. Undernourished gravid females often passed small yolk masses with dead embryos from time to time as much as several weeks before actual birth of their litters. The females seem to have little capacity for the resorption of yolk material. Dolley (1939:170) dissected a gravid copperhead in which the left oviduct contained five embryos and the compacted yolk of an infertile or dead egg. Also, a fully developed dead young of the previous year's brood was found attached ectopically to the intestinal mesentery. On October 7, 1957, I captured a gravid female on the Reservation, well past the time when most normal litters are born. The female appeared undernourished. She died in late November, and still had not produced young. Upon dissection it was found that a yolk mass of an infertile or dead egg, of rubbery consistency, was at the lower end of one oviduct, effectively preventing the passage of fetuses through the birth canal. Dr. Joseph P. Kennedy told me of dissecting a recently caught gravid female and finding all the fetuses dead, malodorous, and partly decomposed.

TABLE 11. BIRTH DATES OF LITTERS OF YOUNG COPPERHEADS IN VARIOUS SAMPLES

PLACE	Number of litters in sample	Average birth date of young	Range of birth dates
1. Kansas—Gloyd (1934), Barton (1948), La Cygne samples in 1958 and 1959	32	Sept. 7	Aug. 23 to Sept. 29
2. Kansas—Reservation in 1950 and 1951	22	Oct. 12	Sept. 17 to Nov. 6
3. Kansas—Reservation in 1949 and 1952 through 1959	40	Sept. 11	Aug. 24 to Oct. 13
Ohio—Conant (1938), New Jersey—Ditmars (1896), Pennsylvania—Barton (1948), Smith (1940), Swanson (1952)	26	Sept. 5	Aug. 9 to Oct. 15
Texas—Allen (1955), Curtis (1949), Guidry (1953), Werler (1951), Oklahoma—Carpenter (1958), Chenoweth (1948)	9	Aug. 21	Aug. 3 to Sept. 4
Louisiana—Clark (1949)	5	Sept. 20	Sept. 10 to Oct. 4
Virginia—Hoffman (1945), North Carolina—Ditmars (1907), West Virginia—Reese (1926)	3	Sept. 4	Aug. 20 to Sept. 13
Connecticut—Finneran (1948), Massachusetts—Babcock (1926)	3	Sept. 10	Sept. 1 to Sept. 29

Geographic differences in the trends are suggested in Table 11. Most litters from Texas and Oklahoma were born in August. Possibly these southern populations emerge from hibernation early, and breed weeks earlier than individuals of northern populations. If so, it is logical that the birth dates of their litters should be relatively early. Each of the seven samples probably contains some litters the gestation of which was unnaturally prolonged in captivity.

Certainly this is true of the litters born on the Reservation in 1950 and 1951.

Extreme effects of unfavorable factors in captivity are shown in the following five females captured many weeks before birth of their litters. The first date is the date of capture and the second is the date of parturition. In 1950: August 2, October 19; July 31, October 31; July 24, October 31; July 8, November 6. In 1951: August 3, October 20. In the same year other females, caught soon before the birth of their litters, were probably little affected by captivity. Summers of both 1950 and 1951 were characterized by subnormal temperatures with unusually heavy precipitation and many overcast days. Perhaps the time of breeding was delayed beyond the normal time. In any event, there can be no doubt that in both 1950 and 1951 gestation periods were extended beyond the usual time in females living under normal conditions. In these years many females were still gravid when captured at dates later than the latest recorded by Gloyd and Barton for parturition of Kansas females. The captures made by me in which parturition occurred later than usual were as follows (first date being that of capture, and second date that of parturition). In 1950: September 17, September 25; September 14, September 24; September 19, September 29; September 9, October 7; September 19, October 13; in 1951: September 17, October 2.

An average parturition date of October 2 is indicated for this group, demonstrating that birth may be delayed for several weeks as a result of unsually cool weather. Making due allowance for delayed births because of low temperatures, and malnutrition in captivity, I regard mid-August to mid-September as the period when most natural births occur, with a trend toward the earlier dates in the more southern parts of the range, and toward the later dates at the northern edge of the range.

Excluding the parturition dates that were obviously delayed, in 1950 and 1951, average dates each year for the eleven years of the study on the Reservation were: 1949—Sept. 18 (3); 1950—Oct. 2 (5); 1951—Sept. 26 (4); 1952—Sept. 2 (4); 1953—Sept. 9 (4); 1954—Sept. 11 (10); 1955—Sept. 9 (1); 1956—Sept. 13 (1); 1957—Sept. 17 (7); 1958—Sept. 15 (9); 1959—Sept. 10 (5).

Number of Young per Litter

Because the copperhead is common in thickly populated regions, and because the gravid female is less secretive than other individuals, much has been published concerning the numbers of young produced. Second-hand records and newspaper accounts of alleged litters numbering 42 to 80 young were discredited by Gloyd (1934:597), but even excluding such records, the literature reflects much difference of opinion concerning the usual number of young per brood. Allen (1868:179), Hay (1892:533) and Stejneger (1895:405) stated that the young number seven to nine. Surface (1906:189) gave the number as six to ten. Ditmars (1910:338) stated that there are about a dozen young per brood, but later (1931:102) gave the number as six to nine and these figures were repeated by Lamson (1935:26). Other statements are: four to nine (Hurter, 1911:208; Stewart, 1929:11; Netting, 1939:132; Gowanloch, 1943:47), three to ten (Necker, 1939:36), two to ten (Wright and Wright, 1957:912, quoting Conant and Bridges, 1939, in "What Snake Is That?", and Davis and Brimley, 1944, in "Poisonous Snakes of the Eastern United States"; Smith, 1956:307), and one to 17 (Wright and Wright, *loc. cit.;* Oliver, 1958:45). Schmidt and Inger (1957:266) stated that the young average no more than six, with ten a maximum. Minton stated that captive females in Indiana produced litters of four to eleven young, and Guidry (1953:55) wrote that in southeastern Texas numerous broods born in captivity averaged five.

Specific records from published literature and from my own field study indicated a total of 1068 eggs or young from 203 females, with an average brood of 5.26 ± .147. From the histogram (Fig. 15) it is evident that broods of four, five and six, in that order, are by far the most frequent, followed by broods of seven and three with relatively few broods having fewer than three (down to just one) or more than seven (up to 14, with one possibly valid record of 17). The trends differ somewhat in different samples within the group. There is some indication of geographic variation in litter size, as shown by the following divisions:

Subspecies *mokeson*, Kansas: 115 litters averaged 5.02 ± .385
Subspecies *mokeson*, eastern states: 55 litters averaged 6.16 ± .283
Subspecies *laticinctus:* 12 litters averaged 5.75 ± .945
Subspecies *contortrix:* 16 litters averaged 6.50 ± .56

The figures listed above are based upon the following litters mentioned in the literature: Allen (1955:228) 5, 5 (Texas); Anderson (1942:215) 5 (Missouri); Atkinson (1901:152) 6 (Pennsylvania); Babcock (1926:5) 6 (Massachusetts); Barbour (1950:106) 3, 6 (Kentucky); Barton (1948:198) 5, 9 (Pennsylvania), 6 (Kansas); Beyer (1898:19) 7 (Louisiana); Brimley (1923:114) 8, 6, 4 (North Carolina); Burger and Smith (1950:432) 5 (Maryland); Carpenter (1958:115) 6, 4, 4, 4, 1 (Oklahoma); Chenoweth (1948:162) 5 (Oklahoma); Clark (1949:259) 10, 7, 7, 6, 6, 5, 5 (Louisiana); Conant (1938:112) 10, 10, 6 (Ohio); Curtis (1949:12) 7 (Texas); Dolley (1939:170) 5 (Mississippi); Dunn (1915:37) 7 (Virginia); Finneran (1948:124), 12, 10, 5 (Connecticut); Gloyd (1934:596) 6, 6, 6, 6, 5, 5, 5, 5, 4, 4, 4, 4, 4, 4, 4, 3, 3, 2, 2, 2 (Kansas); Guidry (1953:55) 6, 5 (Texas); Hoffman, 1945:204) 4 (Virginia); Lynn (1929:97) 7, and McCauley (1945:134) 8, 7, 7, 6, 5, 2 (Maryland); Moski (1954:67) 14 (Connecticut); Neill (1948:161) 11 (Georgia); Smith (1940:80) 10, 9, 7, 7, 5, 5, 5, 5, 5, 5, 5, 5, 4, 4, 3 (Pennsylvania); Stadelman (1928:67) 8 (Pennsylvania); Swanson (1952:176) 6 (Pennsylvania); Werler (1951:46) 4 (Texas); Wright and Wright (1957:906) 7, 6, 5, 4 (New Jersey, citing Hook).

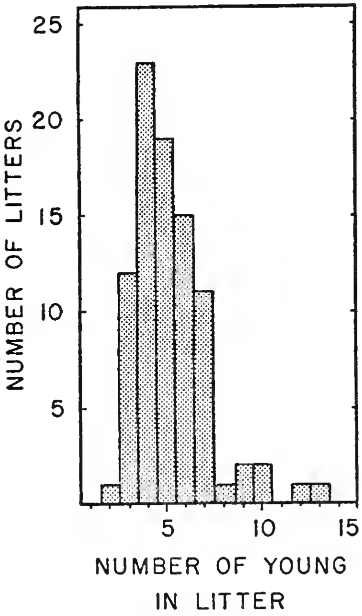

FIG. 15. Numbers of young per litter in copperheads on the area shown in Fig. 1. There are usually three, four, five, six or seven young; litters of fewer than three or more than seven are uncommon, and litters of four are most frequent. In other parts of the geographic range the trends are slightly different.

Within a local population the number of young per litter seems to be proportional to the size of the female. Meager information available concerning geographic variation in size suggests that those populations having individuals genetically larger have more young per litter. In the western part of its range the copperhead, whether of the subspecies *mokeson* or *laticinctus,* is relatively small, and litters were found to be correspondingly small in this region.

There is some chance of bias in the samples, but its effect may be slight. Several records may have been published because they were regarded as exceptional, for example a litter of 14 young mentioned by Moski (1954:67), and one of 13 embryos mentioned by Hurter (1911:208). In my own experience, gravid females kept for periods of weeks in captivity often aborted an occasional embryo, perhaps as a result of injury sustained in capture, or unfavorable conditions in confinement. Possibly similar occurrences went unrecorded in some of the females which later gave birth to the litters recorded by various authors. Although some loss of this type may be normal, the average number of young born at term may have been abnormally low in the samples. Comparison of number of eggs and embryos with number of young actually born bears out

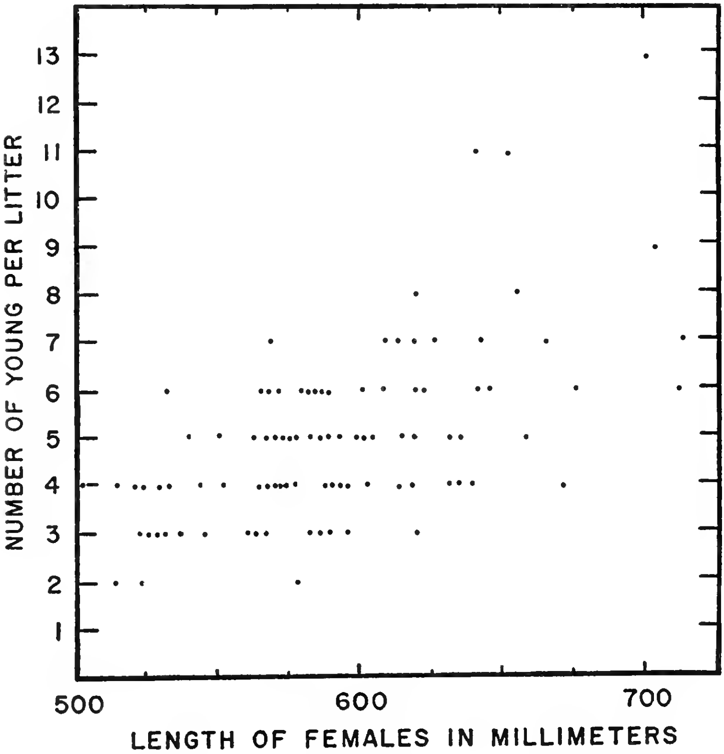

FIG. 16. Number of young per litter in female copperheads of various lengths (shown exclusive of tails), on the area shown in Fig. 1. In general, the larger females have more young per litter, but with much individual variation.

the idea that there was some loss in gestation, but it is not known how much of this loss was normal.

Embryos or late ovarian eggs: 36 litters averaged 6.19 ± .449.
Young born: 162 litters averaged 4.91 ± .164.

There may be local differences in size of litter even within one part of the geographic range. Gloyd (*loc. cit.*) recorded an average of 4.2 young in 20 litters from females collected in Franklin, Miami, Linn, Riley, Marshall and Bourbon counties, Kansas. He noted that on the average these litters contained fewer young than litters reported in the literature from females collected in the eastern states. Many of the females were collected by Vernon Mann in the vicinity of La Cygne, Kansas. In 1958 and 1959 I obtained 16 litters from females collected by Mann near La Cygne. These differ significantly in number of young from the sample collected on the Reservation and immediately adjacent areas.

Gloyd's sample and La Cygne 1958-59 sample: 36 litters averaged 4.03 ± .287.
Reservation: 88 litters averaged 5.25 ± .206.

In Gloyd's sample, and in my own sample from La Cygne, the females averaged small, and I judge most of them to be three-year-olds or four-year-olds, which would produce relatively small litters. Whether these snakes are typical of breeding females in the population represented, or whether some sort of selection was involved in obtaining them is uncertain.

Fig. 16 shows the number of young per litter plotted against size of female. Correlation is evident but the number per litter for each size group of females is subject to wide variation. Females less than 600 mm. in snout-vent length (including nearly all those bearing their first and second litters) usually have from three to six

TABLE 12. AVERAGE NUMBERS OF YOUNG FOR FEMALES OF DIFFERENT SIZE GROUPS

SIZE OF FEMALE (millimeters, snout-to-vent)	Number of litters in sample	Average number of young
700 or more	4	8.75
650 to 699	6	6.66
600 to 649	21	5.66
550 to 599	35	4.57
500 to 549	8	3.62

young; those from 600 to 650 mm. usually have from four to seven young, and the largest females, those of more than 650 mm., usually have from six to thirteen young.

Birth of Young

Actual birth of young copperheads has been described by several observers. Gloyd (1934:593) noted that all but one of the 20 females kept by him underwent parturition at night. One that he kept under close observation during the process moved restlessly about the box, nervously twitching the posterior part of her body. The tail was elevated to an angle of about forty-five degrees and lowered at intervals. Soon a fetus appeared at the cloaca. The posterior third of the snake's body moved slowly from side to side, and a peristaltic wave pushed the fetus backward a few millimeters at a time. When about half extruded, the young snake straightened its neck and thrust its head through the membranes and a continuous wavelike motion of the female's body pushed it smoothly through the remaining distance. The female's only movements, besides those necessary for the expulsion of the fetus, were to flex the neck slightly, and she remained perfectly motionless for twenty minutes afterward. The extrusion of the young snake took slightly less than ten minutes. At birth the young snakes were folded two or three times within the membranes, with their heads toward the middle. The first part presented in the births observed was a bend of the neck. Unless the membranes were ruptured during parturition, the young made no effort to break through it for about forty-five minutes. Gloyd noted that the duration of labor required for expulsion of each young was about ten minutes. Smith (1940:78) reported labor periods of 12, 11, 9, 5 and 6 minutes for the last five of a litter of ten. Intervals between emergences of these young were 16, 15, 19 and 12 minutes.

In the course of my own observations, I found the length of time required for parturition and the time required for the young to rupture their natal membranes, both to be highly variable, depending on temperature, on the condition of the female, and perhaps on other factors. Usually the process extended over many hours, and there was no distinct tendency for births to be concentrated at particular times of the day or night. On September 13, 1954, when air temperature was 23° C. at 8:30 a. m. a large female was found already to have given birth to four of her young. All were still enclosed in fetal membranes. At 8:35 birth of a fifth was completed. At approximately 9:35 the sixth of the litter was born and extrusion of a seventh was completed at 9:55. The eighth was born at 10:40

a. m., and the ninth (and last) at 11:55. In labor the contractions were slight. The posterior end of the body moved slowly from side to side several times, with noticeable contraction of the abdominal muscles. The fetal membranes appeared first, and usually within 20 seconds the fetus had been entirely extruded, although still resting in contact with the female's cloaca.

A large litter of ten young were born in the laboratory on the afternoon of September 3, 1952. At 1:15 p. m. the first young was noticed already about two-thirds emerged from the female's cloaca. By 5:30 p. m. eight more had been born and a ninth was partly extruded. By 9:30 p. m. birth of the tenth and last of the litter was completed. On October 9, 1951, at 8:30 a. m. a female was found to be in labor with two young already born, still enclosed in fetal membranes, beside her. At approximately 3:00 p. m. birth of the sixth and last young was completed.

In most instances the young, extruded still enclosed in their fetal membranes, lay inert for varying lengths of time (Plate 20, fig. 1). In some, spasmodic twitching, especially of the head region, was noticed soon after birth, perhaps stimulated by the pressure of the female's muscular contractions in labor. Often many hours elapsed before the young showed signs of life, especially if air temperature happened to be substantially below the optimum level for activity. In many instances soon after birth of the young I ruptured the membranes artificially with a wire and prodded the snakes. When thus stimulated, they underwent violent muscular contractions, sometimes crawled clumsily a short distance, and immediately became alert, showing awareness of their surroundings and even striking out with poorly directed strokes at any movement in the vicinity. In the young that were left undisturbed, activity was delayed and sometimes began with a lunging motion by which the head was thrust through the enclosing membrane. The young snake was then able to breathe and seemed to become aware of its surroundings but it might remain coiled within the ruptured membrane for several hours subsequently. Several young copperheads that were unusually small and feeble at birth, remained inactive within their natal membranes so long that, with the evaporation of fluids, they were effectively glued to the substrate and would not have been able to escape without aid. Lynn (1929:97) mentioned such an occurrence; the last of a brood of seven born on September 24, 1928, was smaller than the others and was so slow to become active that it was imprisoned within the dried membrane for nine days, and broke loose only when it was moistened.

Behavior of Females

Anderson (1942:215) expressed the opinion that females often remain with the young for several days after birth. Such association seems fairly plausible in view of the fact that the oviparous *Agkistrodon rhodostoma* remains with its eggs and guards them. Anderson reported finding numerous female copperheads under the same rocks with their young. In two instances ecdysis of the young had taken place and in other broods young were nearly ready to shed, suggesting that several or many days had elapsed since parturition. A female was observed in a rock crevice with three young on September 7, 1941, and the group was still together on the following day.

On various occasions I have found litters of young still assembled but not accompanied by the female. In only one instance, on September 24, 1958, have I found a female with a litter. In this instance the female was in the cavity beneath a rotten stump, and she contained a mouse which probably had been eaten since birth of the young. These young were scattered over an area of several square feet, some in the root cavities of the stump and others coiled on the surface, but partly concealed by sheltering vegetation. The young shed two days later. In this and other instances it seemed that dispersal of the family group was delayed not so much by their affinity for each other as by their extreme sluggishness, causing them to remain for long periods in the same spot, or to move such short distances that they remained in the vicinity of the same shelter and returned to it when its protection was required.

Pregnant females were noticeably more docile than other copperheads, but they underwent a noticeable change of disposition after the birth of their litters. They became irritable and would vibrate their tails in response to any disturbance in the vicinity of their cages. When the recently born young were disturbed or removed from the cages containing their mothers, the latter assumed a particularly menacing demeanor, moving toward the disturbance with neck arched and tongue darting rapidly. Although their behavior clearly suggested defense of the young, they usually did not strike, perhaps failing to find a suitable target since the young were removed with wire hooks or metal tongs.

Defects and Mortality at Birth

Among the copperheads born in captivity there were many stillbirths, and deformities were noted from time to time. One snake born while still far short of the usual size, was eyeless, and several others had the spinal column kinked so severely that normal locomotion would have been impossible. The effects of captivity on the females in producing deformity and mortality in young cannot be evaluated, but much of the abnormality probably is congenital and occurs under natural conditions. Klauber (*op. cit.*:699) stated that female rattlesnakes, especially those long captive often produce infertile eggs and dead or defective young. He estimated that, on the average, these defects would eliminate about three eggs or young per litter.

In the copperheads born in captivity stillbirths were probably more frequent than they would have been under natural conditions. Occasional mortality probably resulted from the females lying on their newborn young and crushing them in the close confines of the cage, before the young had become active. Also, the handling involved in capture and transfer, and the conditions of captivity, probably increased the number of deaths and defects in the unborn young. Unfavorably low temperature at the time of parturition may cause mortality in young that are otherwise normal. At 8:30 a. m. on October 9, 1951, after a night with temperature in the forties a female was found to be in labor, with two young already born. Both were still enclosed in fetal sacs, and when the membranes were removed the young remained inert, and apparently lifeless. Later in the day when they had been warmed in the sunshine, one of these young revived, and three of the four young born subsequently also survived. Delayed activity in a young born at low temperature might permit the enclosing membrane to dry, suffocating the snake, or glueing it to the substrate, with fatal results.

The Egg Tooth

Dunn (1915:37) and Gloyd (1934:595) mentioned the presence of an egg tooth in the newborn copperhead. According to Gloyd (*loc. cit.*), "It seems probable that in the ovoviviparous species this structure, of such vital importance in the groups of snakes which produce tough-shelled eggs, is in the process of phylogenetic degeneracy." Although most crotalids are viviparous, it is remarkable that two members of the copperhead's genus, the Malayan pit viper (*Agkistrodon rhodostoma*) and the Chinese pit viper (*A. acutus*) are oviparous. Smith (1943:499) stated, concerning the Malayan pit viper: "Two females kept by me in Bangkok laid 13 and 30 eggs, respectively, on August 1st and September 1st, and guarded them until the young were born, 42 and 47 days later.

Development was already well advanced when the eggs were laid. They measured approximately 32 x 30 mm., and the young when born were 150-160 mm. in length." Even in more specialized and strictly viviparous crotalids, the rattlesnakes, an egg tooth is retained. Klauber (1956:697-698) confirmed its presence in many species and quoted Trapido's (1939:230) observations on newborn timber rattlers which made series of upward thrusts of the head to rupture the fetal membranes in a manner that may have brought the egg tooth into play. Klauber described the rattlesnake's egg tooth, which is situated medially in the front of the upper jaw just behind the recurved and indented edge of the rostral plate. It is so minute as to be scarcely discernible, and its position renders doubtful any functional value.

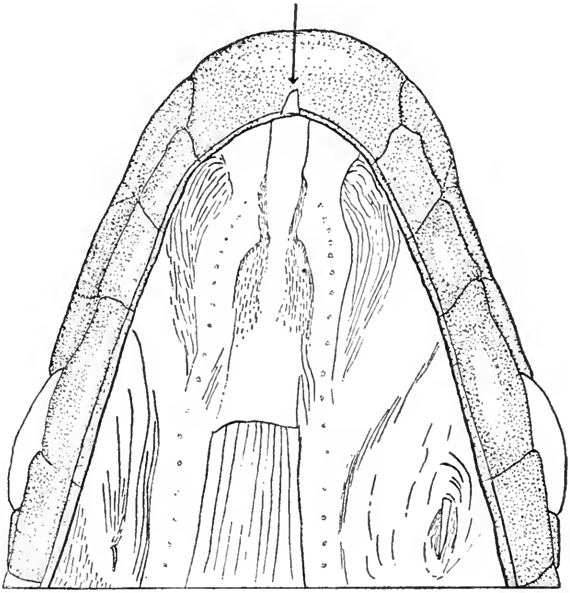

FIG. 17. Palate of newborn copperhead, showing egg-tooth projecting horizontally from the mouth at lower edge of rostral plate, × 7.

In the copperhead, the egg tooth remains functional. In young preserved at birth, it can be easily felt as a thorny projection, when a finger is run lightly over the rostral region. The egg tooth is flattened, chisellike and the tip, which is slightly crenulate, is less than half the diameter of the base (Fig. 17). The tooth is rigidly attached to the palate near the midline just inside the mouth, behind the rostral plate, and is directed forward, lying in a horizontal plane. In some instances the edge of the rostral is slightly wrinkled by the egg tooth pressing against its lower edge. In most observed instances the egg tooth was slightly to the right of the midline. Considerable variation was noted among twelve young or four litters in the shape and position of the egg tooth. One individual had a symmetrical pair of egg teeth. This snake was abnormal in other respects; the eyes were lacking and the facial pit on one side was open ventrally and continuous with the palate. Although relatively smaller than the egg teeth of some oviparous snakes, that of the copperhead is useful in permitting it more easily to puncture the enclosing membrane soon after birth, lessening the chance of suffocation.

Occasionally the fetal sac enclosing the young copperhead was ruptured in parturition, but more frequently it remained intact. Typically, the newborn snake remained inert coiled inside the membrane for from several minutes, to several hours, if the temperature was unusually low. The first sign of life consisted of feeble movements by which the snake oriented its forebody with the dorsal surface upward, and then slowly raised its head. The head, usually situated near the center of the snake's coils, was sometimes directed almost straight upward. Over a period of perhaps half an hour the head would be gradually raised until the snout projected against the enclosing membrane as a distinct protuberance. Although no sudden or vigorous movement had been made, the pressure of the snout against the membrane, perhaps aided by the projecting egg tooth, eventually punctured the membrane and the edges collapsed about the side of the head leaving the nostrils exposed. Then, typically, the little snake remained coiled motionless for several hours, with only its head or snout free of the membrane, permitting it to breathe.

Size at Birth

Size at birth is subject to wide variation. Because many of the litters born in captivity were stunted, their sizes cannot be accepted as typical of those under natural conditions. Twenty-one young were collected in September of different years, and probably had grown but little since birth in most instances. They ranged from 247 to 209 mm. in snout-vent length and averaged 222.7 mm. (223.7 for 15 males and 219.2 for five females). Sex was determined for two hundred and thirty-eight young of 49 litters born in captivity. In 26 litters average length of young exceeded 210 mm., and these young were all considered to be normal. The remaining 23 litters, mostly born in 1950 and 1951, all averaged less than 210 mm. and were stunted in varying degrees.

TABLE 13. SNOUT-VENT LENGTHS (IN MILLIMETERS) OF NEWBORN YOUNG

	Number in sample	Male length	Female length	Female/male length ratio
Normal litters born in captivity...	145	222.5(264–203)	219.0(256–203)	99.1%
Stunted litters born in captivity...	102	194.1(214–170)	190.0(206–160)	97.9%
All captive litters............	247	211.5(264–170)	206 (256–160)	97.3%
Young collected in September......	20	223.7(247–209)	219 (243–210)	97.8%

Forty litters born in captivity contained young of both sexes and the males averaged larger in 29 litters. The female/male length ratio varied from 105.9 per cent to 82.5 per cent in different litters but averaged 98.4 per cent. I conclude that, on the average, females are slightly the smaller at birth.

Appearance of Young

The newborn young are diminutive replicas of the adults in most respects. However, they differ in body proportions. In the young the head is relatively large, and as a result of differential growth in later development, the head of the adult comprises a smaller percentage of its total length and total bulk. The same trend is, of course, equally true of other snakes, and of vertebrates in general. However, the different proportions have implications that apply specifically to the copperhead's way of life; in the juvenal copperhead the amount of venom, and the capacity to inject it deeply are greater than they would be if proportions of the body were those of adults. In young males and females the proportions of the tail and the ratio of its length to the total length are similar, and the differentiation that is characteristic of adults appears later in development.

Coloration also differs from that of the adult in one detail. In newborn young the distal half of the tail is dull greenish yellow dorsally and bright yellow ventrally—a trait shared with various other crotalids. Also, the predominantly brown color of the body is tinged with gray. After shedding occurs, the grayish tinge is lost, but the young still lack the richness of tone characteristic of the adults. The chestnut hourglass markings in adults are delicately shaded, paler in the central areas and intensified along their edges, but those of the young are more uniform in shade. In adult males the coloration is more or less suffused with red or pink, but in the young, and usually also in the adult females, the ground color and markings are brown, with no trace of the reddish suffusion.

GROWTH AND DEVELOPMENT

Utilization of Stored Yolk, and Early Growth

Newborn copperheads have varying amounts of residual yolk material enclosed with them in the fetal membranes. Also, each young snake retains a supply of yolk within its abdominal cavity. Gloyd (1934:600) noted the plump appearance of young during the first few days after birth. He dissected four newborn young and found that yolk within the abdominal cavity ranged from 13.8 to 29.2 per cent of the total weight of the snake. In each of two young dissected at an age of ten days the yolk was reduced to less than half a gram, and in one fifteen days old no yolk was present.

While living on the stored yolk, the young snakes grow rapidly and also lose weight rapidly. In 1957, 1958 and 1959 I measured and weighed 39 young of eight litters just after birth and again after intervals averaging fifteen days. All snakes were kept during the interval in cages where water was available but there was no food. Each snake increased in length and lost weight. At birth the young averaged 216.0 millimeters in snout-vent length and weighed 11.9 grams. After the intervals averaging 15 days, they had gained on the average 12.5 millimeters (5.8 per cent), and lost 1.9 grams (16 per cent). The weight loss in these young, averaging more than one per cent per day, emphasizes their rather precarious situation. They must find food soon if they are to survive. In individuals which become emaciated and weakened, the chances of successful feeding are much reduced.

Later Growth

In newborn copperheads there is wide variation in length and weight (from 264 millimeters and 14.9 grams to 160 millimeters and 7.1 grams) in those born in captivity, but ordinarily somewhat less in nature, since many of the captive females produced stunted young. Although ages of individuals cannot be determined with certainty, the trend of growth during the first year is indicated by the sizes of young at different stages of the season, as shown in Fig. 18. This figure shows that in October and November many young are still of the usual size at birth or but little larger although the average length has increased somewhat. In May and June there are still many young that are within the size range of the newborn and nearly all are within the length range 230 to 275 millimeters. For July and August the sample is especially meager, but during these months growth must be relatively rapid. By September there

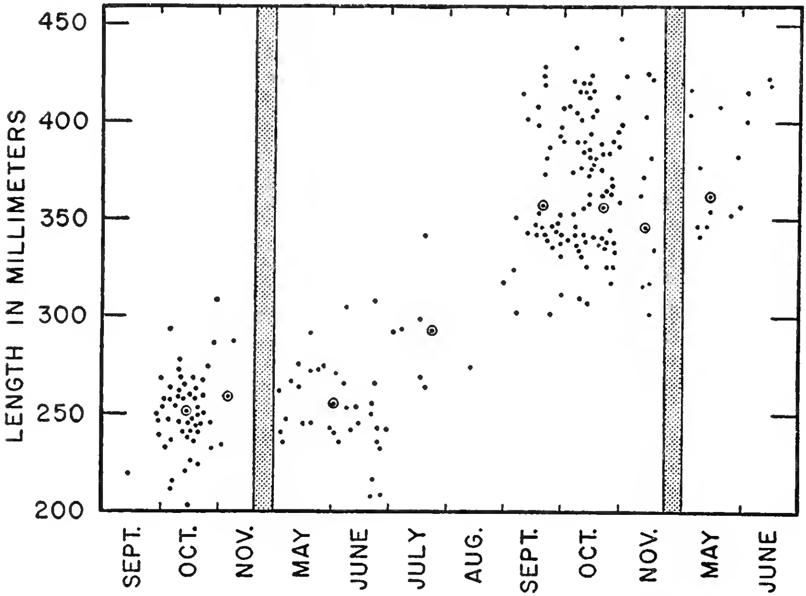

FIG. 18. Lengths (snout-to-vent) of young copperheads caught in their first 21 months on the area shown in Fig. 1. Dots show records of individual snakes and monthly averages are shown by means of dots inside circles. The young are born in September and October, and show considerable variation in size. Those caught in the following May and June, after hibernation, have gained but little. Rapid growth is made during the summer, followed by another period of little or no growth from September to May.

are no young much shorter than 300 millimeters and the largest are more than 400 millimeters. Again during October, November, and the following May the young on the average make little gain. Their growth is probably retarded by cool weather, interrupted activity, and scarcity of food near their hibernation quarters. In early postnatal development there is further divergence, as growth proceeds at different rates, depending upon fortune in finding food, the effects of injuries, disease and parasitism, and the innate size potential of the individual. By the time juvenal copperheads are one year old, some stunted individuals may be no larger than some of the next annual brood which happen to have been born earlier than the usual time, and have made precocious growth. At the other end of the scale, the larger one-year-olds have surpassed the more retarded two-year-olds in size, with wide overlapping between these annual groups. In fact, from the smallest one-year-olds up to adults, the young constitute an almost uniformly graded series, with no major breaks and with no concentrations in any particular size classes. Therefore age cannot be determined by sorting into annual size classes. The only reliable information concerning growth was obtained from the marked individuals released and recaptured. Of particular significance in this regard is a series of 44 copperheads born in captivity, or else captured in fall or in early spring before there was much time to grow beyond the size at birth. The actual or approximate birth dates of these young are therefore known. All of them were recaptured after substantial intervals of up to eight years. Thirteen of the young were undersized at birth and were judged to be stunted as a result of the unnatural effects of captivity on the gravid females. The stunted young probably were somewhat handicapped in their chances for survival by their small size and in other respects. It seems remarkable that so many survived. Whether their growth differed from that of other individuals that were normal at birth is uncertain, but at the time of recapture each appeared normal and healthy, evidently having overcome completely its early handicap. When recaptured, five of the thirteen were still below average size for their ages, but the remaining eight were all above average size for their ages.

In Table 14 showing growth in snout-vent length and in weight, the young are arranged (each sex separately) according to the time elapsed between original capture and recapture. Six were recaptured approximately one year after the time of birth, eleven after two years, six after three years, six after four years, three after five years, and one each after six, seven and eight years.

In adult copperheads, the sexual differential in length is much greater than it is in the newborn, and it increases with advancing age. In the one-year-old and two-year-old snakes likewise the males presumably are the larger. This trend is not evident in my sample, probably because of the small numbers of individuals involved. In both groups females averaged slightly larger; 364 to 338 mm. for the one-year-olds (with a sample of seven) and 480 to 476 mm. for the two-year-olds (in a sample of 20). The female-male length ratio gradually decreases in the older snakes until in those that are seven years old the females average between 84 and 85 per cent of the male's length (snout to vent).

So great is the dispersion in size, that in my small sample the largest two-year-old snake (male) is as long as the smallest eight-year-old (female).

TABLE 14. GAINS IN LENGTH AND WEIGHT IN COPPERHEADS MARKED SOON AFTER BIRTH, AND RECAPTURED IN SUBSEQUENT YEARS

ORIGINAL RECORD			RECORD OF RECAPTURE		
Date	Snout-vent length (mm.)	Weight (grams)	Date	Snout-vent length (mm.)	Weight (grams)
Males					
August 20, 1950	190	....	May 28, 1952	347	....
September 28, 1950	209	12	September 13, 1951	303	25
May 21, 1953	261	11	August 28, 1953	363	36
September 5, 1952	218	11	October 11, 1954	393	38
September 9, 1954	238	13	October 6, 1956	535	60
November 7, 1954	285	....	October 5, 1956	439	....
September 19, 1953	242	13	July 21, 1955	477	72
October 21, 1955	270	16	October 9, 1957	495	75
September 26, 1953	223	10	September 23, 1955	465	71
September 1, 1954	213	11	June 21, 1957	433	55
September 1, 1954	210	9	May 6, 1957	474	62
September 13, 1956	248	14	August 25, 1959	573	115
September 11, 1954	199	11	May 14, 1957	460	....
October 15, 1951	242	12	September 29, 1954	517	79
October 17, 1951	222	10	June 1, 1955	510	118
November 8, 1954	274	11	October 24, 1957	563	90
September 5, 1954	238	13	July 30, 1957	538	71
September 9, 1952	255	16	September 25, 1956	740	255
September 9, 1954	202	8	September 9, 1958	627	138
September 1, 1954	213	10	June 25, 1959	617	115
September 6, 1954	246	15	June 29, 1959	700	178
September 6, 1954	225	16	October 17, 1959	627	141
September 15, 1954	218	13	July 3, 1958	593	100
June 1, 1953	237	....	October 16, 1957	571	114
August 28, 1952	217	12	August 19, 1958	691	192
Females					
August 20, 1950	187	11	September 26, 1951	341	38
August 20, 1950	190	11	May 28, 1952	347	24
September 13, 1954	203	....	September 29, 1955	403	49
May 21, 1953	261	....	August 28, 1953	363	36
August 28, 1952	217	12	October 5, 1954	476	68
September 1, 1954	208	10	April 27, 1957	502	84
September 11, 1954	202	11	April 25, 1957	448	61
September 19, 1953	218	8	June 5, 1957	558	160
September 29, 1955	243	11	June 25, 1958	484	70
September 24, 1950	201	12	October 12, 1954	613	187
September 11, 1954	202	11	June 25, 1958	530	....
September 9, 1954	210	9	June 30, 1959	628	192
September 28, 1950	209	13	August 31, 1955	582	196*
July 19, 1953	239	12	June 4, 1958	536	110
September 6, 1952	222	9	November 1, 1957	622	106
September 6, 1952	241	13	June 1, 1958	606	143
June 20, 1949	265	15	October 10, 1956	622	180
September 29, 1950	191	12	November 2, 1958	644	165

* Gravid.

TABLE 15. GAINS IN LENGTH AND WEIGHT IN COPPERHEADS MARKED BEFORE THEY HAD COMPLETED GROWTH (AND RECAPTURED IN SUBSEQUENT YEARS)

ORIGINAL RECORD				RECORD OF RECAPTURE			
Date	Snout-vent length (mm.)	Weight (grams)	Estimated age in months	Date	Snout-vent length (mm.)	Weight (grams)	Estimated age in months
♂ Sept. 13, 1949	348	31	12	Sept. 28, 1950	431	56	25
♂ Oct. 13, 1954	378	36	13	Oct. 2, 1955	533	112	25
♂ July 2, 1954	421	43	22	Oct. 5, 1954	488	65	25
♀ Oct. 28, 1955	388	43	14	Sept. 5, 1956	503	80	24
♀ Sept. 13, 1949	373	59	12	April 24, 1951	515	102	31
♀ July 16, 1949	413	41	11	June 9, 1951	438	62	21
♂ Sept. 13, 1949	344	26	12	Oct. 2, 1951	635	148	37
♂ Sept. 29, 1949	385	41	13	May 5, 1952	630	195	44
♂ Oct. 5, 1949	486	70	25	Sept. 15, 1950	572	151	36
♂ June 2, 1958	498	68	33	July 20, 1958	522	82	34
♂ June 30, 1951	562	82	34	Sept. 29, 1951	656	210	37
♂ Oct. 23, 1953	390	28	13	Oct. 10, 1955	633	151	37
♂ April 19, 1958	508	73	31	Sept. 30, 1958	600	140	36
♂ May 18, 1957	409	46	20	June 30, 1958	559	109	33
♂ Oct. 21, 1953	474	63	25	Oct. 17, 1954	593	142	37
♂ Oct. 5, 1957	502	......	25	Sept. 20, 1958	597	124	36
♂ Oct. 16, 1956	378	24	13	Oct. 11, 1958	550	90	37
♂ June 5, 1958	433	52	21	Oct. 20, 1959	555	170	37
♂ June 30, 1958	383	36	22	Aug. 4, 1959	518	85	35
♂ Sept. 17, 1958	423	65	24	Oct. 18, 1959	495	82	37
♂ Oct. 10, 1958	420	62	25	Oct. 6, 1959	530	105	37
♂ Oct. 21, 1958	585	99	36	June 2, 1959	625	147	45
♀ June 3, 1950	437	49	21	Sept. 21, 1951	598	220	36
♀ June 11, 1950	335	28	21	Sept. 14, 1951	548	135	36
♀ July 31, 1949	443	56	23	Aug. 28, 1950	485	93	36
♀ Oct. 24, 1951	333	20	13	Oct. 20, 1953	459	58	37
♀ April 19, 1958	472	60	31	Oct. 11, 1958	552	81	37
♀ June 12, 1958	488	77	33	Oct. 16, 1958	508	95	37
♀ Sept. 25, 1957	457	70	24	July 28, 1958	497	65	35
♀ June 5, 1958	433	52	21	Oct. 20, 1959	555	170	37
♀ Sept. 24, 1958	496	86	24	Nov. 4, 1959	590	142	37
♀ Oct. 14, 1958	447	83	25	Aug. 5, 1959	536	112	35
♂ Oct. 23, 1957	544	100	37	May 26, 1958	570	98	45
♂ Sept. 29, 1949	458	53	24	Sept. 26, 1951	696	240	48
♂ Nov. 12, 1954	427	52	26	Oct. 13, 1956	628	147	49
♂ Oct. 14, 1955	592	135	37	Oct. 13, 1956	655	141	49
♂ Oct. 24, 1957	603	128	37	Sept. 24, 1958	688	200	48
♂ Oct. 5, 1957	544	......	37	Sept. 24, 1958	630	160	48
♂ Oct. 16, 1956	378	24	13	Nov. 3, 1959	608	130	50
♂ Oct. 2, 1957	458	60	25	Sept. 24, 1959	613	125	48
♂ June 5, 1958	511	73	33	Nov. 4, 1959	645	165	50
♂ Aug. 15, 1958	523	94	35	Sept. 16, 1959	620	155	48
♂ Oct. 16, 1958	533	100	37	Aug. 15, 1959	660	137	47
♂ Sept. 29, 1949	385	41	12	May 5, 1952	630	195	44
♀ April 20, 1955	558	132	43	Oct. 8, 1955	601	90	49
♀ Oct. 3, 1949	432	52	25	Oct. 18, 1951	630	222	49

TABLE 15. GAINS IN LENGTH AND WEIGHT IN COPPERHEADS MARKED BEFORE THEY HAD COMPLETED GROWTH (AND RECAPTURED IN SUBSEQUENT YEARS)—*Continued*

ORIGINAL RECORD				RECORD OF RECAPTURE			
Date	Snout-vent length (mm.)	Weight (grams)	Estimated age in months	Date	Snout-vent length (mm.)	Weight (grams)	Estimated age in months
♀ June 30, 1951	553	94	45	Sept. 27, 1951	603	168	48
♀ June 14, 1955	525	120	33	May 11, 1956	550	111	44
♀ Sept. 17, 1958	525	100	36	Sept. 26, 1959	647	185	48
♂ Aug. 5, 1950	578	136	35	May 20, 1952	660	210	57
♂ Sept. 27, 1951	543	125	36	May 20, 1953	643	162	57
♂ Oct. 23, 1953	474	63	25	Oct. 16, 1956	710	190	61
♂ May 5, 1950	663	128	55	Oct. 17, 1950	674	174	61
♂ Sept. 23, 1952	637	149	48	Sept. 5, 1953	672	200	60
♂ Oct. 2, 1955	656	166	49	Oct. 14, 1956	692	190	61
♂ May 11, 1958	662	130	56	Oct. 20, 1958	675	168	61
♂ Sept. 27, 1957	623	150	48	Sept. 20, 1958	635	134	60
♂ Oct. 7, 1956	590	112	37	Sept. 27, 1958	692	230	60
♂ Oct. 31, 1953	425	48	25	Sept. 23, 1956	691	182	60
♂ Oct. 3, 1950	647	175	49	Oct. 2, 1951	758	260	61
♂ Nov. 12, 1954	427	52	26	Oct. 31, 1957	658	185	61
♂ Oct. 5, 1957	544	......	37	Sept. 24, 1959	683	220	61
♂ July 28, 1958	600	121	47	Aug. 4, 1959	665	200	59
♀ June 11, 1950	335	28	21	Oct. 17, 1953	634	134	61
♂ Oct. 17, 1950	506	102	37	Aug. 12, 1952	574	248	59
♀ Oct. 13, 1951	477	78	25	July 6, 1954	595	203	58
♀ Oct. 15, 1952	589	95	49	Sept. 19, 1953	648	189	60
♀ Aug. 29, 1949	525	96	36	Aug. 24, 1951	616	228	59
♀ Oct. 10, 1949	570	137	49	Aug. 5, 1950	574	177	59
♀ June 27, 1955	505	103	22	June 16, 1958	595	121	57
♀ July 15, 1958	584	148	58	Oct. 20, 1958	620	173	61
♀ May 22, 1952	580	182	54	Nov. 5, 1952	610	173	62
♀ Oct. 7, 1955	537	102	37	May 16, 1958	620	160	67
♀ June 27, 1955	505	103	22	June 16, 1958	595	121	58
♀ May 14, 1957	486	51	32	Oct. 9, 1959	603	165	61
♀ Nov. 7, 1958	554	112	49	Oct. 27, 1959	580	140	61
♂ Oct. 11, 1949	663	198	49	May 19, 1951	734	272	68
♂ Sept. 23, 1952	670	169	60	Sept. 7, 1953	728	200	72
♂ July 14, 1956	623	......	46	July 3, 1958	655	150	70
♂ Oct. 8, 1955	529	90	25	May 20, 1959	688	165	68
♂ Oct. 7, 1956	590	112	37	Nov. 3, 1959	748	280	74
♀ Sept. 28, 1950	583	192	48	June 24, 1952	645	303	69
♀ Sept. 30, 1950	574	211	48	Aug. 12, 1952	653	343	71
♀ Oct. 4, 1951	442	52	25	Sept. 9, 1955	637	183	72
♀ Oct. 10, 1949	603	85	61	July 7, 1950	600	230*	70
♀ June 8, 1956	608	238*	69	Sept. 13, 1956	617	160	72
♀ June 20, 1955	519	146	33	Oct. 20, 1958	670	214	69
♀ June 27, 1951	593	230	46	Sept. 26, 1953	623	206	72
♀ Oct. 17, 1956	513	68	37	Oct. 27, 1959	597	142	73
♂ July 14, 1956	623	......	46	June 21, 1959	658	165	81

Table 15. Gains in Length and Weight in Copperheads Marked Before They Had Completed Growth (and Recaptured in Subsequent Years)—*Concluded*

Original Record				Record of Recapture			
Date	Snout-vent length (mm.)	Weight (grams)	Estimated age in months	Date	Snout-vent length (mm.)	Weight (grams)	Estimated age in months
♂ Oct. 5, 1949	630	141	49	Aug. 30, 1952	791	316	84
♂ May 31, 1953	721	233	81	Sept. 4, 1953	757	256	84
♂ Sept. 19, 1953	728	220	60	July 27, 1955	770	273	83
♂ Sept. 13, 1955	713	221	72	Oct. 13, 1956	733	242	85
♂ Sept. 17, 1955	678	150	60	Sept. 27, 1957	709	200	85
♂ Sept. 16, 1954	630	155	48	Oct. 4, 1957	720	228	85
♂ Oct. 17, 1953	448	58	25	June 20, 1959	760	238	93
♂ Sept. 27, 1958	686	218	72	Oct. 27, 1959	709	222	85
♀ Oct. 17, 1950	506	102	37	July 11, 1954	585	237	82
♀ June 27, 1951	593	133	58	Sept. 26, 1953	623	207	82
♀ Oct. 1, 1951	584	112	49	Sept. 29, 1954	660	222	82
♀ Oct. 10, 1949	615	85	73	Aug. 5, 1950	620	249	81
♀ April 15, 1950	618	68	77	Aug. 5, 1950	628	246	81
♂ Aug. 19, 1950	617	172	47	May 3, 1955	892	300	104
♂ Sept. 2, 1950	351	28	12	Sept. 24, 1958	838	350	108
♂ Oct. 21, 1953	474	63	25	Oct. 15, 1959	783	295	97
♀ Sept. 30, 1950	574	211	48	Aug. 28, 1954	685	361*	96
♀ May 12, 1952	628	188	91	Oct. 22, 1952	665	210	96
♀ Aug. 20, 1950	580	169	47	July 11, 1954	574	218	94
♀ Oct. 13, 1951	477	70	25	June 3, 1958	645	125	105
♀ Oct. 17, 1953	550	98	37	Oct. 30, 1958	660	183	97
♀ April 20, 1955	558	132	43	Oct. 17, 1959	623	130	97
♂ Oct. 11, 1949	663	198	49	Oct. 1, 1955	898	447	121
♂ Sept. 17, 1951	615	160	36	Oct. 20, 1958	836	268	121
♂ Oct. 5, 1954	776	238	97	Oct. 7, 1958	810	290	144
♂ Oct. 11, 1949	663	198	49	May 14, 1957	890	......	140
♂ Sept. 17, 1952	785	310	96	Sept. 18, 1957	808	272	156
♂ Oct. 7, 1951	715	222	73	Sept. 20, 1958	873	360	156
♂ Oct. 24, 1951	765	415	85	Oct. 24, 1957	955	476	157
♂ Oct. 4, 1953	793	300	......	Sept. 22, 1959	838	417	168

* Gravid.

From the figures in the foregoing table it is evident that males grow faster than females, especially in the fourth years, that four-year-olds are of typical adult size, and that the snakes from five to eight years old are mostly somewhat above average adult size but far short of maximum size. Wide variation in growth rate exists, between individuals as well as between the sexes.

Many other copperheads were caught and marked when they were already partly grown, and were recaptured after substantial intervals. Although the ages of these individuals are not determinable with certainty, data from the foregoing table reveals the trend in early growth. For instance an individual captured in autumn having a length of more than 300 millimeters and less than 400 millimeters is almost certainly a one-year-old, and any individual

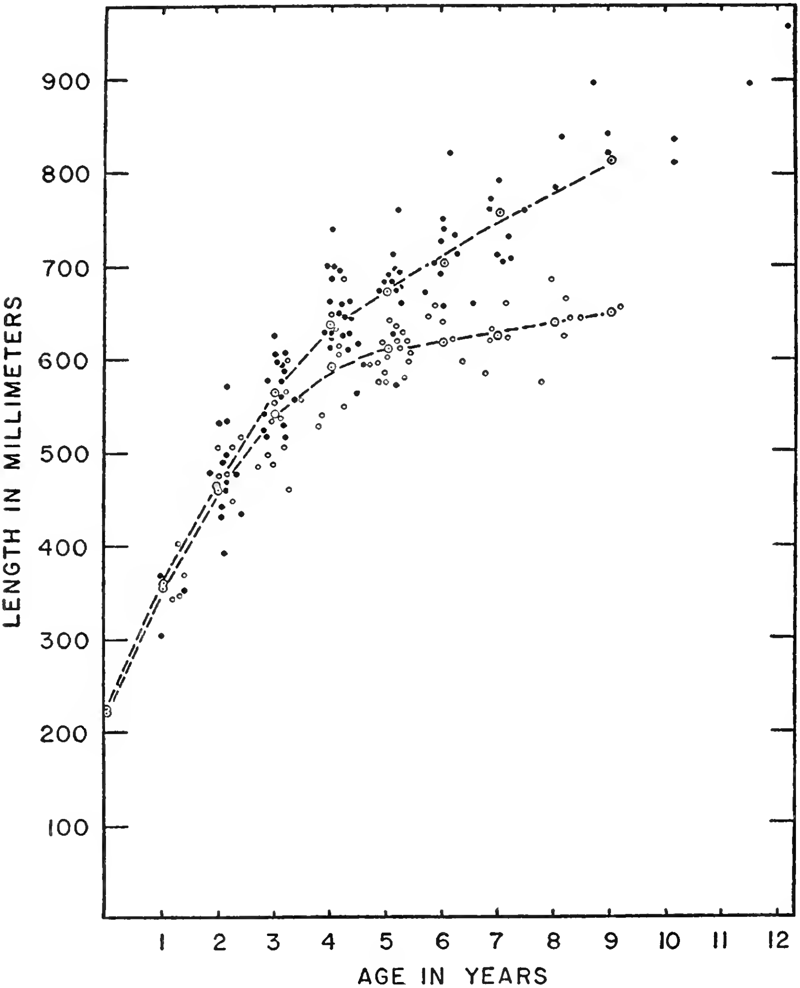

FIG. 19. Lengths (snout-to-vent) in recaptured marked copperheads of known ages from the area shown in Fig. 1. Solid circles represent males and open circles represent females. Circles that enclose dots represent averages for age groups, and are shown separately for males and females. The curves of growth differ but little between the sexes for the first two years. In the third year, growth in females is markedly slowed and in the fourth year females fall even farther behind males. After the fourth year females make relatively small annual gains, while growth slackens much more gradually in the males.

up to average adult size can similarly be assigned a "probable age" and identified with one of the annual age classes. For such individuals marked, and then captured again after substantial intervals, the original estimated age plus the time elapsed between captures provides an indication of the ages corresponding to various sizes of subadult and adult snakes. For those already adult when marked there is a greater element of uncertainty as to exact age, but even conservative estimates indicate ages up to 14 years for some of the largest copperheads recaptured.

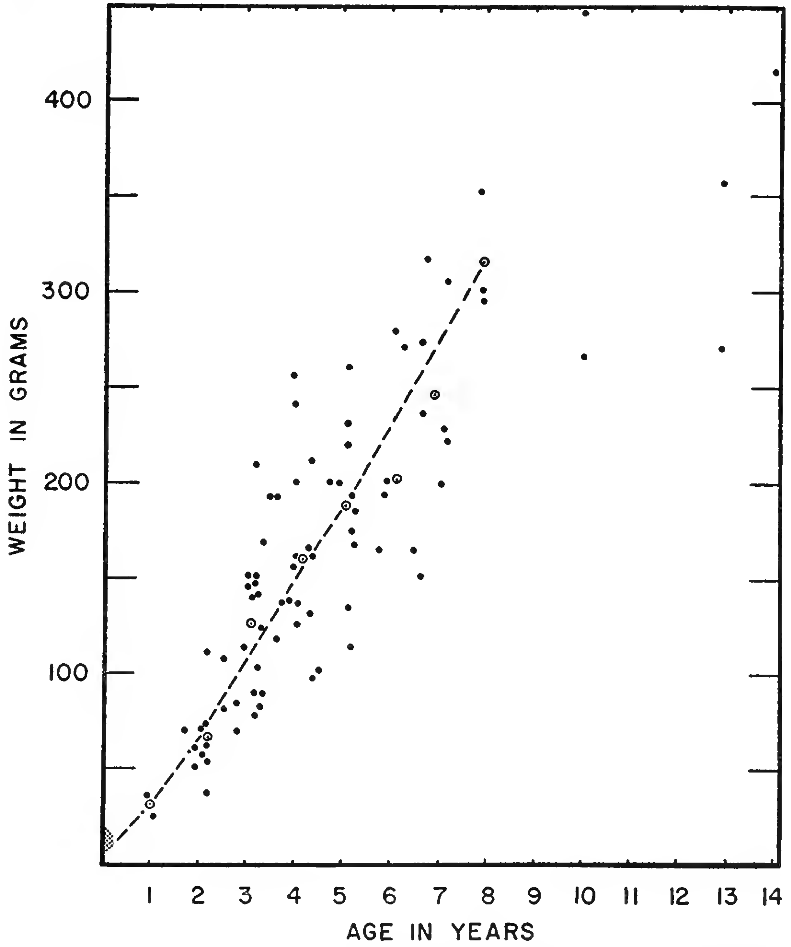

FIG. 20. Weight in recaptured marked male copperheads, from area shown in Fig. 1, whose ages were known definitely or approximately. The general trend is for weight to increase rapidly from year to year, even in those individuals that have attained sexual maturity.

Cessation of Growth

In contrast to the majority of recaptured snakes, including all those listed above, a few individuals recaptured after substantial intervals failed to make any growth or grew but little. Some of these were old adults that were already near maximum size and had slowed their growth rates to a minimum level. Others, far short of adult size may have been handicapped by periods of adversity. In some instances the measurement obtained at recapture was actually less than the original measurement. In measuring the elastic body of a live copperhead, the normal range of error was in the neighborhood of one per cent, but occasionally errors as great as three per cent were made. The trends of the combined length and weight records reflect the vicissitudes of the individual's career.

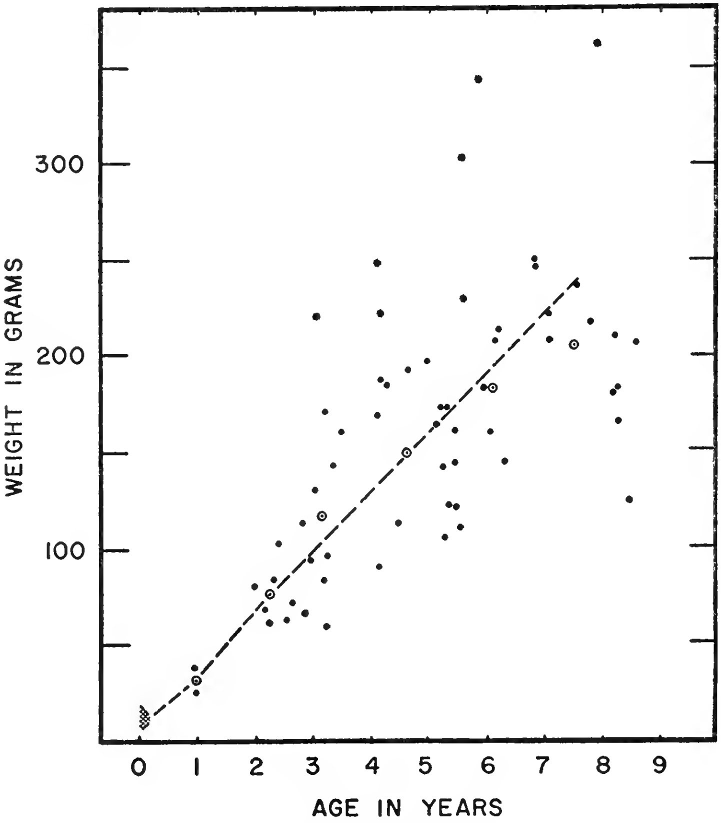

FIG. 21. Weights in recaptured marked female copperheads of known ages. Circles enclosing dots represent averages for age-groups. Asterisks represent females that were obviously gravid, and these individuals are not included in the averages.

TABLE 16. RECORDS OF COPPERHEADS CAPTURED AND MARKED AS ADULTS, WHICH HAD MADE LITTLE OR NO GROWTH WHEN RECAPTURED IN SUBSEQUENT YEARS

ORIGINAL RECORD			RECORD OF RECAPTURE		
Date	Snout-vent length (mm.)	Weight (grams)	Date	Snout-vent length (mm.)	Weight (grams)
Males					
July 3, 1958	655	150	June 21, 1959	658	165
September 27, 1957	623	150	September 20, 1958	635	134
September 17, 1955	678	150	September 27, 1957	709	200
October 5, 1954	765	238	October 7, 1958	810	290
September 17, 1952	779	288	September 14, 1954	733	302
September 17, 1952	785	310	September 18, 1957	808	272
October 13, 1956	790	276	May 10, 1958	788	....
May 3, 1955	792	286	October 16, 1957	801	300
July 14, 1958	778	335	July 12, 1959	800	375
October 4, 1953	793	300	September 22, 1959	838	417
May 27, 1958	920	400	October 12, 1959	910	350
Females					
June 11, 1957	556	168	July 22, 1958	574	133
September 20, 1955	573	96	November 11, 1958	590	90
September 7, 1957	590	191	September 1, 1958	578	218
October 8, 1955	601	90	October 17, 1959	623	130
October 15, 1957	670	130	October 17, 1959	663	190
July 5, 1954	700	329	September 9, 1957	685	247

FOOD HABITS

Method of Obtaining Prey

Food is obtained by ambush. Lying silent and motionless for long periods with shorter intervals of slow and stealthy prowling, the snake is likely to be overlooked by prey animals but is alerted to their approach by sight or scent or differential temperature detected by the pit. The facial pit is found in all crotalids; its development may be primarily an adaptation for hunting in darkness, and also for hunting warm-blooded prey. However, the organ is able to detect objects of low temperature as well as those that are high. Bullock and Cowles (1952:542) stated that the pit has outstanding sensitivity to radiant heat. The threshold of sensitivity is indicated by stimulation by the human hand at a distance of 30 cm. The neutral point is independent of bodily temperature and depends on the average radiation from all objects in the receptive field. Objects that are colder than their surroundings depress nerve activity, even if they are warmer than the body and are thus fully as noticeable to the snake as warm objects. The receptive field is an irregular cone extending in the horizontal plane about 10° across the midline in front and almost at right angles to the body laterally from the pit. Bullock and Fox (1957:231) have described in detail the anatomy of the pit, and have related it to function in sensing the presence and position of prospective prey. Receptor nerve endings average only two to five microns beneath the epidermal surface inside the pit permitting prompt response, and detection of flickering and brief stimuli. The authors explain that because the pit's diameter is constricted at its mouth, radiant objects will not illuminate the whole sensory membrane but will cast shadows of the pit margin. This confers the possibility of deriving information about the direction of small objects or the edges of large objects.

In captivity copperheads that were offered rodents struck and invariably snapped back into a coiled position immediately, releasing the prey. In such situations it seemed that the snake's response to the rodent's presence was in part defensive, and in the confines of a small cage the behavior toward prey may not be representative of that under natural conditions. Various authors have suggested that behavior of the copperhead differs in dealing with different kinds of prey and that some types are struck and released while others are held until the venom takes effect. Instantaneous release of the animal struck usually ensures that the prey will not deliver a retaliatory bite, which might entail serious injury or death to the snake; however, such release might often result in loss of the prey, which would wander too far to be found.

Several authors have expressed the opinion that the copperhead characteristically retains its hold after striking a bird or frog, which might be irretrievably lost upon release, but that the snake withdraws from biting a mammal. Conant (1938:112) concluded from observations at the Toledo Zoo that large and active prey is bitten and released, whereas smaller prey is retained in the jaws and helpless victims such as newborn mice are engulfed without being bitten, except that the fangs are employed to help work the food down the throat. McCauley (1945:135) reached essentially the same conclusions. Davis' (1938:183) record of a copperhead catching a white-throated sparrow is perhaps the only detailed observation of predation on a bird under natural conditions, and it bears out the supposition that the snake retains its hold awaiting death of the bird.

I have never seen a copperhead catch prey under natural conditions. On September 8, 1948, a half-grown copperhead found coiled in leaf litter was offered a dead shrew held in steel forceps. When the shrew had been pushed slowly toward the snake to within 1½ inches, the snake suddenly turned its head toward the shrew and almost instantly struck at it, biting hard just behind the head and retaining its hold. For two minutes the snake did not shift this original grip, but rested motionless except for slight movements of its jaws as it strove to embed its fangs more deeply, and injected venom. It then began swallowing the shrew without ever having released it. Swallowing was completed approximately 20 minutes from the time the bite was delivered. The behavior of this individual was probably representative of those ambushing prey under natural conditions. A shrew or mouse struck and pierced through the thoracic, abdominal or cranial cavities might succumb in a few seconds. Fast-moving small prey animals such as cicadas, skinks and birds would usually escape if released and must ordinarily be held in the jaws after the original stroke. The innate caution and nervousness of the copperhead probably causes it to release any prey animal that struggles effectively and shows signs of retaliating, while feebler prey is held down and immobilized until the venom subdues it.

On June 22, 1960, when newly metamorphosed bullfrogs were numerous along the margins of the pond on the Reservation, my sons observed a large copperhead that was actively prowling at mid-morning. The sky was overcast and humidity was high. When first seen the snake was swimming near the shore line. For approximately six minutes that it was watched it continued to swim or to crawl rapidly along the edge of the water. On four occasions it left the shore line to head for a bullfrog (a different one each time) resting on algae out in the water, and approached the frog with rapid, purposeful movements. Each time, the frog jumped while the snake was at least six inches away, and the snake struck in a futile attempt to secure it. The observers were watching from a boat, approximately 15 feet from shore. In the course of its wandering, the snake came up against the side of the boat and swam along it attempting to by-pass the obstruction but when one of the observers moved, the snake suddenly took alarm, swam rapidly to shore, and escaped into dense vegetation.

The feeding of captive individuals may give erroneous impressions regarding the habits under natural conditions. Of the many individuals kept by me for varying lengths of time in captivity, few would eat regularly even though preferred natural foods such as voles, white-footed mice or ring-necked snakes were offered.

Most of the food left in the cages was wasted, and when the food supply was limited, force-feeding was usually resorted to despite the fact that it involved some hazard to both the snake and the handler. Risk of injuries to the snakes were reduced by skinning the carcasses to be fed to them, thereby reducing friction as the food was forced into the mouth and down the gullet. Strips of raw beef were found to be much more easily swallowed by the snakes and the latter seemed to thrive as well on this diet as on natural foods. John A. Knouse informed me that several of a group of copperheads that he kept were induced to take raw hamburger that had been warmed and offered on the end of a spatula. The acceptance of warmed hamburger is significant in connection with the copperhead's preference for warm-blooded prey.

Beyer (1898:23) wrote that copperheads kept by him became tame ". . . learning to take food, such as pieces of meat and fish from the fingers" and he stated that these snakes preferred fish over beef. Gloyd (1928:132) wrote that the copperheads he kept fed well on rats, mice, and sparrows but none showed the slightest interest in fish or frogs. In Ohio, Conant (1938:112) also found that captives readily ate mice and sparrows but none took frogs of the several species that were offered. Nevertheless in Indiana, Minton (1944:475) found that the young would eat small frogs. In Maryland, McCauley (1945:135) found that captives would eat frogs and salamanders as well as birds and mammals. In eastern Oklahoma, Chenoweth (1948:162) found that young copperheads ate small cricket frogs but refused small mice. In southeastern Texas, Guidry (1953:55) found that captives would feed fairly well on mice and small birds but would refuse frogs and toads.

Luring of Prey by Young

The yellow tips of the tails of juveniles may serve as lures to attract prey. Ditmars (1907:424) wrote "Quite frequently, when food is introduced into a cage containing small Copperheads, the tails of the little snakes wriggle and twist in a manner that instantly suggests their remarkable similarity to yellow grubs or maggots. When among dried leaves the colours of the young snakes blend so perfectly with their surroundings that it is almost impossible when a little distance away, to discover them with the exception of the bright yellow tail." Neill (1948:161) confirmed this idea with a litter of 11 young from a female caught near Augusta, Georgia. The young were placed in a wooden box with leaf litter, and several cricket frogs (*Acris crepitans*) were introduced. The box was left in one corner of a room, covered so that the interior was partly darkened. Later, peering into the shadowy interior, Neill saw ". . . a number of writhing, yellowish objects, for all the world like small worms or maggots . . . each little copperhead was coiled up and was holding aloft its bright yellow tail, which was writhing slowly." When the frogs became alarmed, and leaped about the container, the snakes wriggled their tails with increased vigor. In confinement the frogs were not interested in feeding and none actually fell prey to the copperheads.

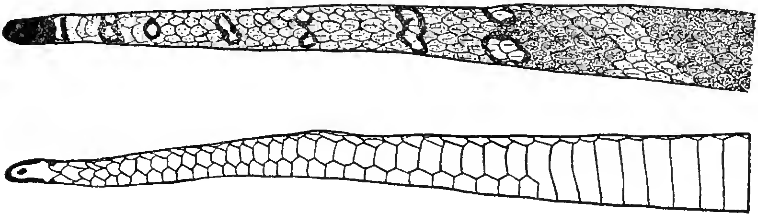

FIG. 22. Distal half of the tail of a newborn copperhead from dorsal and ventral views, × 5. The distal one-fourth of the tail is bright yellow ventrally, and dusky yellow with conspicuous markings dorsally.

I have kept several dozen broods of young copperheads, and have often introduced small vertebrates, such as frogs, lizards, snakes or shrews, into the containers with them as prospective food. On many occasions these animals have been struck and killed, and sometimes they have been eaten, but I have never succeeded in eliciting the tail-waving behavior described by Ditmars and Neill. Therefore I infer that the response is less strongly developed in the local population that I have studied than in populations in some other parts of the range. Possibly strength of the reaction is correlated with frog-eating habits, as suggested by Burger and Smith (1950:432). Frog-eating certainly is less prominent in the northwestern population of copperheads than in some others from elsewhere in the range.

At any rate, there can be no doubt that the brightly colored tail in the juvenal *Agkistrodon* is correlated with luring behavior to obtain prey, and that the reaction is more strongly developed in some other members of the genus than it is in the copperhead. Allen (1949:225) published a remarkable photograph illustrating tail-waving in juveniles of the Mexican cantil (*A. bilineatus*), and described in detail the behavior of these snakes. "The tail was bright yellow for 3 cm. from the tip and on both sides, and the extreme end was grey, giving an unmistakable appearance of a yellow caterpillar with a [grey] head. . . . The juvenile . . . carries its tail in a vertical position with the yellow tip in intermittent motion. It resembles nothing so much as a wriggling worm twisting about hungrily in search of food." The juvenal cantils kept by Allen successfully lured and struck various small animals placed in their container, including tree-frogs (*Hyla*) of different species, oak toads (*Bufo quercicus*) and an anole (*Anolis carolinensis*?) but usually they did not feed, and eventually starved. Even when the young cantils were at rest, with no prey in the vicinity, the tails were normally held elevated from 2 to 2½ inches (one-fourth to one-fifth of the total length) and were set actively in motion when prospective prey was near. Allen noted that the tails were kept down for two days in individuals that had fed, and also were lowered at night.

Henry (1924:257) made observations on a litter of the hump-nosed viper (*A. hypnale*) of India which showed that in this species also the tail is used effectively as a lure. When a small skink (*Lygosoma*) was introduced ". . . their tails, which were of a whitish colour, were protruded from the coils and caused to wriggle about in an extraordinary manner, looking for all the world like so many very active earthworms . . . whenever a small lizard of any kind was put into the cage, the tail-wriggling immediately commenced. . . . On several occasions I saw small geckos actually seize a snake's wriggling tail and instantly receive a fatal wound from the venomous little creature."

Statements of Food Preferences

Many authors have made statements concerning the food habits of the copperhead. Some of these doubtless were based on original observations, but unfortunately cannot readily be separated from statements that merely reiterate the findings of earlier writers.

". . . their food [in New York] consists of birds, frogs, mice, and even squirrels, which they catch by surprise as they do not climb trees" (Rafinesque, 1819:86).

"Its usual food seems to be small birds and field mice. . . ." (Holbrook, 1838:71.)

"Slugs, birds and mice have been found in their stomachs. . . ." (Atkinson, 1901:152, in Allegheny County, Pennsylvania; the finding of slugs in the food has not been corroborated.)

". . . their food [in Texas] consists of small rodents, lizards, frogs. . . ." (Mitchell, 1903:27.)

"The feeding habits are rather eccentric and seemingly relate to the possibility of finding certain kinds of food during different phases of the season. . . . During the spring and fall it is very fond of frogs. . . . During the later spring, these snakes prefer young birds, showing in fact such a decided preference to this food that some snakes will fast unless provided with the feathered prey. During the summer months captive specimens will eat small rodents, such as mice and rats, or chipmunks." (Ditmars, 1907:424.)

"The food consists of frogs, small birds and rodents." (Ditmars, 1910:338.)

"Small rodents, birds and frogs." (Lamson, 1935:26.)

". . . known to eat mice, squirrels, shrews, birds, frogs, insects, salamanders and even opossums." (Gowanloch, 1943:47.)

". . . it feeds [in spring] mostly on mammals . . . in the summer . . . large numbers of frogs and insects are consumed in addition to mammals." (Oliver, 1955:174.)

"The catholic appetite is satisfied by small warm-blooded animals as well as small cold-blooded ones that even include insects" (Pope, 1955:224).

"The food consists chiefly of mice, with occasional birds, and even large insects and larvae of insects." (Smith, 1956:306.)

"Its food consists mainly of small mammals, but when large insects, like some caterpillars, are available, they are regularly taken." (Schmidt and Inger, 1957:266.)

"Small rodents, small birds, frogs" [subspecies *contortrix*]; "Small rodents, lizards, frogs, toads" [subspecies *laticinctus*]; "Small mammals, birds, insects, toads, salamanders, but mainly rodents and insects" [subspecies *mokeson*] (Wright and Wright, 1957:906-913).

Composition of the Diet

Of the 589 prey items identified in my study, 77 were from scats collected in the large cage at La Cygne, Kansas, where Vernon Mann had kept many copperheads and smaller numbers of several other kinds of snakes. Because these La Cygne scats could not be identified with individual snakes and a few of them may have been produced by snakes other than copperheads their records have been kept separate from those of the scats definitely known to have been produced by copperheads.

Among the 512 items in the known copperhead scats and from stomachs of copperheads there were: 90 prairie voles (*Microtus ochrogaster*), 80 cicadas (*Tibicen pruinosa*), 66 white-footed mice (mostly *Peromyscus leucopus*, though a few were definitely identified as *P. maniculatus* and many were identified only to genus), 39 short-tailed shrews (*Blarina brevicauda*), 35 ring-necked snakes (*Diadophis punctatus*), 33 little short-tailed shrews (*Cryptotis parva*), 30 five-lined skinks (*Eumeces fasciatus*), 29 caterpillars (*Actias luna*, *Celerio* ? and several other saturnids and sphingids not definitely identified), 24 pine voles (*Microtus pinetorum*), 18 harvest mice (*Reithrodontomys megalotis*, and possibly one or more *R. montanus*), 13 narrow-mouthed toads (*Gastrophryne olivacea*), 8 frogs (*Rana pipiens* and possibly others), 6 jumping mice (*Zapus hudsonius*), 6 slender glass lizards (*Ophisaurus attenuatus*), 6 cotton rats (*Sigmodon hispidus*), 4 each of worm snake (*Carphophis amoenus*), and house mouse (*Mus musculus*), 3 each of brown skink (*Lygosoma laterale*), and common garter snake (*Thamnophis sirtalis*), 2 each of racer (*Coluber constrictor*), eastern wood rat (*Neotoma floridana*), eastern cottontail (*Sylvilagus

TABLE 17. ESTIMATED PERCENTAGES, BY WEIGHT, OF VARIOUS PREY SPECIES IN THE DIET OF THE COPPERHEAD AT TWO LOCALITIES IN EASTERN KANSAS

KIND OF PREY	Weight of individual prey item in grams	Percentage by weight of sample	
		Reservation	La Cygne
Prairie vole	30	38.6	1.4
White-footed mouse	18	16.3	6.0
Pine vole	30	10.5	4.3
Short-tailed shrew	12	6.7	2.3
Cotton rat	40	3.5	13.4
Ring-necked snake	6	3.1	.3
Five-lined skink	7	2.8	1.3
Little short-tailed shrew	6	2.5	.3
Harvest mouse	10	2.5	....
Cicada	2	2.1	.5
Jumping mouse	15	1.3	....
Eastern wood rat	40	1.2	1.9
Eastern cottontail	40	1.2	65.0
Luna and other moth larvae	2	.6	.3
Narrow-mouthed toad	4	.7	.2
Glass lizard	10	.9	.5
House mouse	15	.6	.7
Bird	20	.3	1.0
Common garter snake	10	.3	.5
Leopard frog	10	2.9	....
Other	....	1.4	.1
		100.0	100.0

floridanus), De Kay's snake (*Storeria dekayi*) and bird (*Richmondena cardinalis?*, *Spinus tristis?*) and one each of hatchling box turtle (*Terrapene ornata*), Great Plains skink (*Eumeces obsoletus*), six-lined racerunner (*Cnemidophorus sexlineatus*), black rat snake (*Elaphe obsoleta*) and unidentified snake.

Of the 77 items in the scats from La Cygne, 34 were cottontails, 7 were white-footed mice, 7 were cotton rats, 6 were cicadas, 4 were short-tailed shrews, 4 were five-lined skinks, 3 were pine voles, 3 were caterpillars, and there were one each of prairie vole, little short-tailed shrew, ring-necked snake, narrow-mouthed toad, glass lizard, common garter snake, wood rat, house mouse, and bird (*Agelaius* ?). Since the snakes had not been fed in captivity, these prey items represent natural feeding.

In the copperhead, meals are relatively large and infrequent and the prey is invariably swallowed entire. Since the various prey species differ greatly in size, composition of the diet is best shown by calculating the percentage by bulk of each species in the total food consumed (Table 17).

Kinds of Prey

In this study the prairie vole proved to be by far the most important species in the copperhead's diet, with more than twice the biomass of any other species. On the Reservation this vole is by far the most abundant small mammal (Martin, 1956:376; Fitch, 1957:131). By 1958 more than half the Reservation's area provided habitat favorable for the vole. The grassy and weedy fields where prairie voles occurred were of irregular shapes and were well distributed over the Reservation. No point was more than 500 feet from such habitat, and probably almost every copperhead had voles within its home range. Spring dispersal of copperheads from the rock ledges in woodland where they hibernate to grassland habitat is perhaps motivated by the abundance of the voles in the grasslands. At all ages and sizes the voles provide food for adult copperheads but the voles are in varying degrees unavailable to the younger snakes, which depend largely on other kinds of prey. The vole's habit of keeping to well-defined runways renders it easy prey for the copperhead, which often lies in or beside runways motionless but ready to ambush any small mammal that may come within reach. By day, when temperature is unfavorably high and humidity low the vole's burrows provide underground shelter for the copperheads in grassland habitat.

The pine vole is relatively uncommon on the Reservation and at times may be less than one per cent of the prairie vole's numbers (Fitch, 1958:80). In view of its relative scarcity, the pine vole is eaten with surprising frequency. In habitat and in over-all geographic range it corresponds closely with the copperhead. Over the copperhead's range as a whole, it is possibly the one most important food source. Surface (1906:189) found meadow voles (*Microtus pennsylvanicus*) in 13 stomachs of copperheads from Pennsylvania. In Virginia, Uhler, Cottam and Clarke (1939:610) found microtines of four kinds in 20 stomachs; the meadow vole, pine vole, red-backed mouse (*Clethrionomys gapperi*) and southern bog lemming (*Synaptomys cooperi*). Hamilton and Pollack (1955:3) recorded one pine vole in a stomach from Georgia. Bush (1959:76) found pine vole (one individual?) to comprise one-sixth by bulk of the total sample from six Kentucky copperheads that contained food.

"Mice" collectively including two species of white-footed mice, harvest mice, jumping mouse and house mouse, were next in importance to voles. The white-footed mouse (*Peromyscus leucopus*) prefers the same woodland and edge habitat occupied by the copperhead, and is generally abundant over much of the copperhead's range. Therefore this mouse is probably a major food source. This mouse prefers the same sort of rock ledge situation which the copperhead chooses for hibernation, and as a result it figures in some of the earliest and latest seasonal records of the copperhead's feeding. As it averages only a little more than half the size of a vole, this mouse is available as food to copperheads over a wider range of size. The deer mouse was tentatively identified in 12 occurrences. It is limited to small areas of the Reservation, where vegetation is sparse. Most of the occurrences of "*Peromyscus* sp." doubtless pertained to the commoner and more generally distributed white-footed mouse. The harvest mouse because of its relatively small size, is available as food even to young copperheads except those of the smallest size groups. Harvest mice were taken more often than mice of any other kinds except those of the genus *Peromyscus*, reflecting their abundance and extensive habitat on the Reservation. The interspersion of grassland and woodland habitats on this area favors predation by the copperhead on this grass-living rodent, but elsewhere harvest mice probably figure less importantly. The geographic ranges of the copperhead and the western harvest mouse overlap but little. The range of the eastern harvest mouse (*R. humulis*) is largely within that of the copperhead but there are no definite records of predation on this species. The meadow jumping mouse occurred six times among the food items identified from the Reservation. The range of this mouse overlaps almost the northern half of the copperheads' range, and the habitats of the mouse and the snake are similar. The house mouse occurred four times among the recorded items, but probably comprises only a small part of the diet over the entire range. Uhler, Cottam and Clarke (*loc. cit.*) found white-footed mice (*Peromyscus* sp.) in seven digestive tracts and a meadow jumping mouse in one. McCauley (1945:135) recorded a white-footed mouse, a house mouse and a meadow jumping mouse in stomachs of specimens from Maryland. Clark (1949:259) recorded 15 mice, species undetermined, among the stomach contents of 55 copperheads from Louisiana. Barbour (1950:106) found a jumping mouse (*Napaeozapus insignis*) in one of two copperheads examined from Big Black Mountain, Kentucky. Hamilton and Pollack (*loc. cit.*) found a white-footed mouse (*Peromyscus* sp.) in one stomach and cotton rats in four. Bush (1959:76) recorded that white-footed mice (two individuals?) comprised 58.3 per cent of the total sample in six copperheads from Kentucky that contained food. Surface (*loc. cit.*) found a white-footed mouse in one stomach, house mice in two others, unidentified mice in three, and unidentified mammals in three.

Rats made up only 1.6 per cent of the items recorded from the Reservation. The eastern wood rat was scarce on the area for most of the period of the study. The cotton rat was abundant in 1958 and 1959 but relatively scarce in some other years. Rat-sized rodents, when fully adult, are too large to be swallowed by any but the largest copperheads. However, during the summer, the bulk of the population consists of immature individuals. In the outdoor enclosure where copperheads were kept, partly grown cotton rats were eaten avidly whenever they were offered. There were no sciurids among the items identified in my study, but Uhler, Cottam and Clarke (*loc. cit.*) found chipmunks (*Tamias striatus*) in two and an unidentified squirrel in one. Surface (*loc. cit.*) also recorded an unidentified squirrel in one stomach. He also recorded opossums (*Didelphis marsupialis*) from three. These latter records are remarkable, since a young opossum at the time it first emerges from the mother's pouch, is already a large morsel for an adult copperhead.

Rabbits make up a variable but sometimes important part of the diet. On the Reservation only one occurrence of the cottontail was recorded among the total of 512 items even though cottontails were common on the area. But in the samples from La Cygne 34 of the 77 items were cottontails. The snakes from which these scats were obtained were mostly gravid females which were collected in August, along woodland rock ledges. Perhaps cottontails were unusually numerous at this particular time and place. Only young in the nest during their first week or two would be small enough to be eaten by a copperhead, and the snake would need to be fully adult. The eastern cottontail and other rabbits of the same genus occur throughout the copperhead's range and their young may constitute an appreciable percentage of the food.

The shrews, *Blarina brevicauda* and *Cryptotis parva,* represented by 72 occurrences, constitute an important part of the diet, especially for immature copperheads. The smaller kinds of shrews (*Cryptotis* and *Sorex*) are almost the only mammals within the range of the copperhead that are small enough to be eaten as adults by the youngest snakes. Both *Blarina* and *Cryptotis* coincide approximately with the copperhead in their geographic ranges and *Blarina* has almost the same habitat preferences. The shrews are both diurnal and nocturnal in their activities, and occur in the same type of dense cover used by the copperheads. Surface recorded a short-tailed shrew in one and an unidentified shrew in another. Conant (1938:112) reported a half-grown hairy-tailed mole (*Parascalops breweri*) eaten by a copperhead in Licking County, Ohio. Uhler, Cottam and Clarke (*loc. cit.*) found shrews, including the short-tailed shrew, little short-tailed shrew and masked shrew (*Sorex cinereus*) in the stomachs of eleven of the copperheads from Virginia that they examined. McCauley (*loc. cit.*) recorded a short-tailed shrew from a specimen from Maryland. Barbour (*loc. cit.*) found a shrew (*Sorex* sp.) in one of the two examined from Harlan County, Kentucky.

Small snakes were found 48 times in my samples, and proved to be important in the food of young copperheads. They were chiefly the ring-necked snake, which is by far the most abundant reptile of the Reservation, and is estimated to occur in population densities of ten or more per acre over extensive areas (Fitch, 1958:79). In captivity the ring-necked snake was almost the only prey taken voluntarily by juvenal copperheads. Ring-necked snakes seemed remarkably susceptible to the copperhead's venom; in less than a minute after being bitten they were incapable of normal locomotion, and would die after violent contortions, over a period of minutes. Other small snakes eaten include the worm snake, De Kay's snake, and young of the garter snake, racer and black rat snake. These and many other kinds are available throughout most of the copperhead's range. Probably any small snakes are taken more or less indiscriminately. Surface (*loc. cit.*) reported a milk snake (*Lampropeltis doliata*) in the stomach of one from Pennsylvania. Hamilton and Pollack (*loc. cit.*) reported a crowned snake (*Tantilla coronata*) in the food. Barton (*loc. cit.*) reported an instance of a juvenal copperhead born in captivity which ate a small water snake (*Natrix rhombifera*). Six days later the copperhead died with the other snake's tail still protruding from its mouth.

Of the lizards eaten, the five-lined skink, ground skink, Great Plains skink and glass lizard were taken in much different quantities. The five-lined skink was sixth in number of all the species of prey taken. It is remarkably abundant in woodland and edge habitat; an estimate of 67 per acre was made for a 2¼-acre study area (Fitch, 1958:78). The relatively scarce ground skink, Great Plains skink and glass lizard were taken by copperheads on the Reservation in smaller numbers somewhat proportional to their abundance. Lizards are eaten chiefly by immature copperheads. Up to at least half-grown size, five-lined skinks can be swallowed easily by newborn copperheads, and constitute an important source of food for them. Vernon Mann (in conversation April 29, 1958) mentioned finding a young copperhead in the act of swallowing a five-lined skink near La Cygne. Uhler, Cottam and Clarke (*loc. cit.*) found a fence lizard (*Sceloporus undulatus*) in one of the 105 copperheads from Virginia examined by them. Minton (1944:475) recorded that a copperhead from Indiana disgorged a large fence lizard. Hamilton and Pollack (*loc. cit.*) reported undetermined lizards (*Cnemidophorus, Sceloporus, Eumeces* or *Lygosoma*) in two. Bush (*loc. cit.*) reported *Lygosoma* (two individuals?) comprising 16.5 per cent of the total sample of food from six copperheads from Kentucky. Robert G. Webb in an unpublished thesis in the University of Oklahoma Library, recorded that a copperhead from Comanche County, Oklahoma, contained a collared lizard in its stomach.

Amphibians would seem to be one of the most available food sources. After summer rains copperheads are most active and at the same time dispersing frogs and toads, mostly juveniles, swarm over the fields and woodlands. Opportunities to feed upon them must occur frequently. It must be concluded that amphibians are low on the scale of preference since few were found in the snakes and most of these were the Great Plains narrow-mouthed toad (*Gastrophryne olivacea*). Anderson (1942:216) recorded finding a juvenal copperhead in the act of swallowing one of these toads in Jackson County, Missouri. This small, terrestrial, and partly subterranean toad is numerous in the copperhead's habitat, but at times is much outnumbered by *Bufo, Acris* and *Rana*. Most identifications of narrow-mouthed toads were made from ants (*Crematogaster* sp.) in the scats, as the toads themselves had been completely digested. One leopard frog (*Rana pipiens*) was found in a stomach. It is doubtful whether frogs would have left any remains that would have been recognizable in the scats. As already mentioned, remains of insects of kinds that probably would not have been eaten by the snakes were usually associated in the scats with remains of insectivorous vertebrates—mice, shrews, and lizards—in most instances. The seven instances in which they were not so associated were tentatively allocated as frogs, probably the leopard frog, but possibly including some of the other ranid, hylid, or pelobatid anurans occurring on the Reservation. Vernon Mann told me of finding a copperhead eating a small bullfrog (*Rana catesbeiana*) when he was attracted to the spot by the squalling of the frog. Among 55 items found in stomachs of copperheads in northern Louisiana, Clark (*loc. cit.*) found 30 frogs—22 *Rana pipiens*, seven *R. clamitans*, and one *R. catesbeiana*. Frogs seemed to be much higher on the copperhead's scale of preference in Louisiana than they are in Kansas. Surface (*loc. cit.*) found two slimy salamanders (*Plethodon glutinosus*) in the stomachs of a series of 52 from Pennsylvania. Uhler, Cottam and Clarke (*loc. cit.*) found frogs (*Rana* sp.) in the stomachs of two (of 105) from Virginia. These same authors found eight slimy salamanders, one red-backed salamander (*Plethodon cinereus*), and one red salamander (*Pseudotriton ruber*) in the same series.

"Bird" was represented by three occurrences in my records, each of a different species. Because the remains of feathers were meager and in poor condition, definite specific determinations could not be made, but in each instance the color provided a clue. One scat from La Cygne, Kansas, in August, 1958, contained black feathers, which probably were those of a red-winged blackbird (*Agelaius*) or cowbird (*Molothrus*). Contents of the digestive tract of a large male copperhead caught six miles east and one mile south of Arkansas City, Kansas, on June 1, 1954, contained yellow feathers that may have been those of a goldfinch (*Spinus americanus*) but possibly were from some kind of warbler. The remaining scat, from a copperhead caught on the Reservation on October 22, 1949, contained red feathers, which almost certainly were those of a cardinal (*Richmondena cardinalis*). Opportunity to prey upon birds probably comes when fledgings still unable to fly or climb effectively are wandering about on the ground. Several kinds that share the copperhead's woodland habitat on the Reservation and seem especially vulnerable in this regard are the yellow-billed cuckoo (*Coccyzus americanus*), whip-poor-will (*Caprimulgus vociferus*), Carolina wren (*Thryothorus ludovicianus*), Kentucky warbler (*Oporornis formosus*), summer tanager (*Piranga rubra*), cowbird (*Molothrus ater*), red-eyed towhee (*Pipilo erythrophthalmus*), cardinal, and field sparrow (*Spizella pusilla*).

Davis (1938:183) observed an instance of predation by a copperhead on a white-throated sparrow (*Zonotrichia albicollis*), near Bastrop, Texas, on February 27, 1938. Thrashing movements among dead leaves drew the attention of the observer to the bird, still struggling, its head in the grip of the copperhead, which periodically clamped its jaws tighter as if to embed its fangs more deeply or inject more venom into the prey. The sparrow's struggles soon became feebler, and in three minutes it was limp and lifeless. The snake attempted to drag its prey back into a pile of litter, but released it when disturbed. Wintering flocks of this and various other sparrows are probably subject to but little predation by copperheads because the snakes are normally hibernating at least throughout most of the birds' sojourn in their range. Surface (*loc. cit.*) recorded a fringillid "sparrow" in the stomach of a copperhead from Pennsylvania. Uhler, Cottam and Clarke (*loc. cit.*) recorded six occurrences of birds, including unidentified passerines, a warbler (*Dendroica* sp.) and a ruby-throated hummingbird (*Archilochus colubris*), in digestive tracts of 105 copperheads from Virginia examined by them. How a copperhead might secure such elusive prey as a hummingbird, or even a warbler, is a matter for speculation. Clark (*loc. cit.*) recorded ten birds (species undetermined) in his total of 55 food items from copperheads collected in northern Louisiana.

In one exceptional instance a hatchling box turtle (*Terrapene ornata*) was found in the digestive tract of a large adult male copperhead, the same one, from near Arkansas City, Kansas, that had eaten a bird tentatively identified as a goldfinch. This snake also had in its stomach remains of two voles and a racer, more separate items than occurred in any other specimen. The irregular shape and protective armor of a turtle would render it difficult to swallow for any copperhead except an exceptionally large one. Eating of this

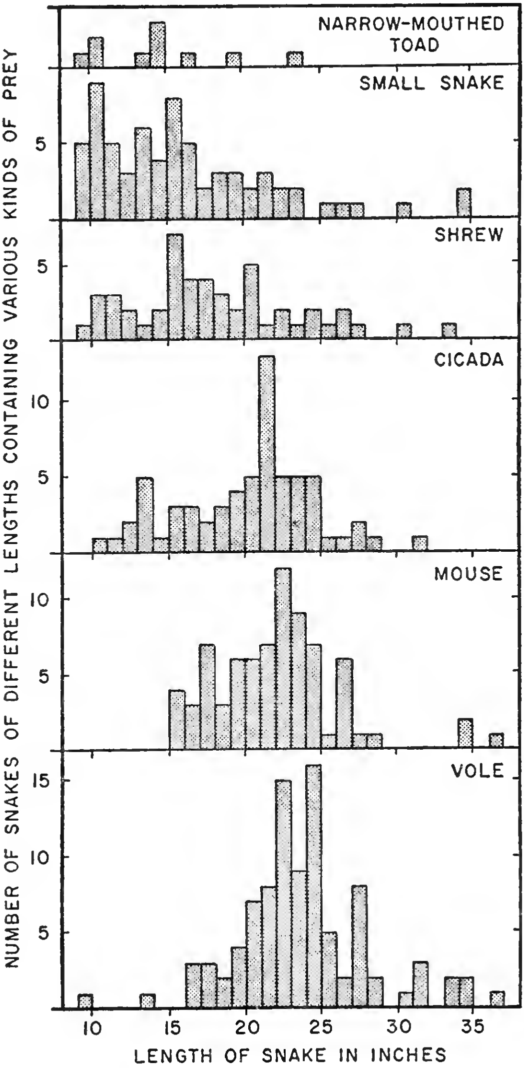

Fig. 23. Differences in food of copperheads of different sizes. Voles and mice are eaten chiefly by adults. Cicadas are eaten by copperheads of all sizes, but most often by adults, whereas shrews (*Blarina* and *Cryptotis*), narrow-mouthed toads, and especially small snakes such as the ring-neck (*Diadophis*) are eaten chiefly by the first-year young.

hatchling box turtle indicates a certain versatility on the part of the copperhead in its choice of prey. Hamilton and Pollack (*loc. cit.*) found three small musk turtles (*Sternothaerus odoratus*) in a large adult male copperhead from Georgia.

Insects that were primary prey items were easily distinguished from those that were secondary (prey of the animals eaten by the snakes) in most instances. They were of larger kinds and were more nearly intact. The common cicada (*Tibicen pruinosa*) was the favorite insect prey, with 80 recorded occurrences, and was second in frequency only to the prairie vole among the many kinds of prey eaten. Although many species of cicadas occur on the Reservation, only this one common species was definitely recorded in the food. Like other kinds of cicadas, *Tibicen pruinosa* has a long period of development; the nymphs remain underground for many years feeding on roots of trees. The nymphs emerge and metamorphose in the latter half of the summer and the adults die with the advent of cold weather in late autumn. Ordinarily the nymphs are unavailable to copperheads throughout the period of their underground existence. The adults likewise are usually safe because of their wariness and their habit of perching several feet above ground. They are vulnerable mainly within a period of a few hours when the nymphs emerge to metamorphose. They crawl about slowly on the ground and then often climb onto a vertical surface such as a rock, stem, or tree trunk. The emerging imago is soft and helpless at first. Ten of the cicadas recorded as food of copperheads were nymphs, all full-sized and probably caught by the snakes soon after they had emerged to metamorphose. Probably most of the imagos eaten were caught soon after metamorphosis, before they had had time to dry thoroughly. Many cicadas of the same brood may emerge at about the same time within a few square yards, and their total biomass is great. Atkinson (1901:152) found five nymphs of cicadas in the stomach of a copperhead from Allegheny County, Pennsylvania. In the same state Surface (*loc. cit.*) found stomachs of six gorged with seventeen-year cicadas (*Magicicada septendecim*). Gloyd (1928:132) wrote that a copperhead collected by him near Gould's Ford in Kansas had eaten several soft-bodied cicadas just transformed. Conant (*loc. cit.*) examined a copperhead in the Carnegie Museum from Washington County, Ohio, that had eaten a seventeen-year cicada that worked its way through the neck of the snake, causing the latter's death. In Dallas County, Texas, Curtis (1949:12) found several copperheads climbing in low trees and shrubs, and upon dissecting the snakes, found them to be gorged with cicadas. McCauley (*loc. cit.*) reported "periodical" cicadas in the food of copperheads in Maryland. Gehlbach (1956: 370) reported that a copperhead found in Santa Elena Canyon, Brewster County, Texas, in mid-June, voided remains of both nymphal and adult cicadas. The cicadas were numerous in the tall grass among limestone slabs where the snake was discovered. Robert G. Webb in "The Reptiles of Oklahoma," an unpublished manuscript in the University of Oklahoma Library, recorded that three of five copperheads caught about 10 p. m., had each eaten two cicada nymphs.

Besides cicadas the only insects eaten regularly by copperheads are lepidopterous larvae of the families Sphingidae, Citheroniidae, Saturnidae, Ceratocampidae, and perhaps others. These accounted for 29 occurrences in my samples. On October 12, 1951, a larva, three inches long, of a sphinx moth (*Celerio?*) was found in the stomach of a small copperhead that had died in a trap. Three larvae of the luna moth (*Actias luna*) were found in the stomach of a copperhead collected in Polk County, Texas, on October 18, 1958. One of these larvae had begun to pupate and was partly enclosed in its cocoon, and probably the snake that ate it found it by scent. Other recorded occurrences of lepidopterans were all from scats, and the remains were inadequate for specific or generic determinations. Adult moths have not been recorded in the natural food of copperheads. When a large hawk moth was released in a cage with two of the snakes, both showed unusual animation, alertly following the movements of the fluttering moth and lunging at it whenever it came within reach. One snake soon caught the moth and ate it. This three-year-old copperhead had been reared in captivity and had been sustained entirely by force-feeding, as it would not accept other kinds of prey that had been offered on various occasions. Several times subsequently hawk moths were offered to caged copperheads, and were always avidly pursued and eaten. When smaller moths were introduced into the cages, the snakes watched them with seeming interest, turning their heads to follow the movements of the moths, but not attempting to catch them.

Surface (*loc. cit.*) found larvae of the polyphemus moth (*Telea polyphemus*) in digestive tracts of two copperheads, of the io moth (*Automerus io*) in two, of the oak worm (*Anisota*) in two, of the imperial moth (*Eacles imperialis*) and the regal moth (*Citheronia regalis*) each in one. Uhler, Cottam and Clarke (*loc. cit.*) found caterpillars of seven genera in 28 of the 105 copperheads they examined from Virginia. Orth (1939:54) found larvae of sphingid moths in the stomach of an adult copperhead from Harriman State Park, New York. Orth offered the larva of a polyphemus moth to a half-grown copperhead in captivity, and the snake soon ate it. Malnate (1944:731) found a nymphalid caterpillar in the stomach of a copperhead from South Carolina. Barbour (*loc. cit.*) found a sphingid larva in the stomach of one (of two) from Harlan County, Kentucky. Hamilton and Pollack (*loc. cit.*) reported a lepidopteran larva in one of 16 from Fort Benning, Georgia. McCauley (*loc. cit.*) reported caterpillars in the food of copperheads in Maryland. Bush (*loc. cit.*) also reported unidentified caterpillars, in a food sample from Kentucky.

It is curious that insects so dissimilar as cicadas and larvae of large moths are highly preferred foods while other kinds of arthropods are rarely taken. Remains of a katydid were present in one scat, but they were in fragmentary condition and probably the katydid had first been eaten by a frog. Carpenter (*loc. cit.*) found that a large male copperhead in Oklahoma contained a spider in its stomach, and McCauley (*loc. cit.*) reported spiders as part of the food in Maryland. Hamilton and Pollack (*loc. cit.*) found a mantis (*Stegomantis*) and a locust (*Scudderia*) in the stomachs they examined and both these large insects were considered to be primary food items since no other prey was associated with them.

Neill and Allen (1956:172) questioned whether the mantis and locust recorded by Hamilton and Pollack were actually primary food items. The former authors cited instances of amphibians eaten by snakes being almost completely digested, while the insect prey ingested by the amphibians remained relatively intact. The spiders recorded in the food by McCauley and Carpenter might similarly be suspect as secondary items even though no remains of vertebrates were associated with them.

Amount of Food Consumed

Poikilothermal vertebrates in general and snakes in particular have low metabolism and their food requirements are correspondingly small. Doubtless there are important differences in quantitative food requirements between different types of snakes. Although no studies of this subject have been made, active and nervous snakes such as racers might be expected to require more food than sluggish kinds such as the copperhead. Certainly racers feed much oftener. Temperature affects the food requirements; in the locality of my study the snakes hibernate for more than half the year, fasting throughout this period and losing but little weight. Even in those parts of spring and fall that are included in the season of activity, food requirements are much reduced because of relatively low temperatures especially at night.

Digestibility of the type of food taken also affects the quantities required. When cicadas are eaten, the heavy exoskeletons are sometimes voided nearly intact. The chitin making up much of the biomass in such prey, is largely resistant to the digestive secretions of the snake, while some other kinds of prey, such as frogs, are so completely digested that no recognizable traces remain. The residue in dried feces from such prey is scanty and is of powdery consistency and dark greenish brown or nearly black.

Crotalids, including the copperhead, are especially well adapted for fasting as compared with other snakes. The normal interval between successive meals is relatively long, the prey is large, and the snakes have the capacity to store quantities of fat in the abdominal cavity. This fat supply is drawn upon in times of enforced fasting, and the snake can fast for several weeks without deteriorating noticeably in condition. A copperhead can survive for much longer periods of fasting but gradually becomes emaciated. Surface (1906:124) recorded one that lived for a year and three months in captivity without feeding. Carr (1926:104) wrote of one caught on July 7, 1924, that would not feed in captivity and was still fasting on June 17, 1925, although it had been active throughout the winter. Klauber (1956:650) mentioned fasts in rattlesnakes of several species at the San Diego Zoo, at a year-round temperature near 80° F., of: 23 months, 19 months, 16 months, 16 months, 16 months, 16 months and 15 months. Copperheads of similar sizes might survive as long. Since there is no need for food and but little loss of weight in winter hibernation, it is conceivable (but improbable) that an individual under natural conditions might live for three years or more without taking any food. Young individuals certainly would starve to death much sooner.

The normal food consumption is incompletely known, but certainly the interval between meals is irregular, and the amount eaten at one time is highly variable. One basis for estimating the average food consumption is the rate of digestion in captive individuals and the proportion of those captured that have food in their stomachs or intestines. Another basis is provided by the amount of food consumed by captive copperheads. In one born in captivity and reared to adult size, weight fluctuation and amounts of food consumed (chiefly through force-feeding) in a six-month period that corresponded to the maximum extent of a season of activity in this locality are shown in Table 18.

TABLE 18. FOOD AND WEIGHT OF A CAPTIVE COPPERHEAD IN 1957

DATE	How food was ingested	Kind of food	Weight of food in grams	Weight of snake in grams
April 15	fed	mouse	14	257
April 25	fed	beef	9	254
May 6	fed	vole	28	280
May 24	ate	2 mice	34	....
June 8	ate	mouse	17	....
June 23	fed	beef	10	257
July 18	ate	rat	26	254
July 30	fed	beef	12	....
August 5	fed	beef	5	....
September 6	fed	glass-lizard	18	....
October 27	fed	beef and mouse	44	238

During the period covered by these records the snake gained in snout-vent length from 585 to 620 mm. Throughout, it was overweight, and a weight of a little more than half its average would have been typical for non-gravid individuals of the same length and sex. By the summer of 1958 this snake was fully adult and it made little gain during the summer. It was recorded to be 630 mm. long on May 20 and 634 mm. on October 22. The food taken in this period is shown in Table 19.

TABLE 19. FOOD AND WEIGHT OF A CAPTIVE COPPERHEAD IN 1958

DATE	How food was ingested	Kind of food	Weight of food in grams	Weight of snake in grams
May 20	fed	beef	29	221
June 20	ate	rat	35	....
July 18	fed	beef	10	234
July 25	ate	rat	12	....
September 11	ate	rat	37	....
October 22	....	....	....	240

In this five-month period spanning the normal season of activity for copperheads locally, this individual consumed only a little more than half the equivalent of its own body weight. Nevertheless it made a slight net gain.

Klauber (1956:631) stated that mature rattlesnakes in captivity thrive on an adequate meal (presumably of about one-fourth the body weight) every 14 to 18 days, and that young need to feed somewhat more frequently to thrive. For them a weekly feeding was considered desirable. He speculated that in the wild, requirements might be somewhat increased because of the more active life, with greater expenditure of energy. Klauber (*op. cit.*:647) further stated that the annual food requirement in captive adult rattlesnakes, that were active throughout the year, amounted to approximately 4½ times the snakes' body weights, and he implied that approximately half that amount might suffice for those in the wild having a long period of hibernation annually.

Copperheads, being closely related to rattlesnakes and somewhat like them in habits, probably have similar food requirements. Less than one-fourth of the snakes captured in my study were recorded to have anything in their digestive tracts. However, in the early years of the study the snakes were not thoroughly tested for food residues in their hind guts. Also the bulk of my records were obtained along the hibernation ledges in fall when the snakes were much less inclined to feed than they were in summer. In the periods June 1 to October 1 in 1958 and 1959 combined, 336 captures were recorded and in these snakes 186 prey items were obtained from scats and only 28 items were obtained from stomachs. In six instances the same kind of animal and presumably the same individual was recorded from both the stomach and the scat. In these instances the food palped from the stomach was partly disintegrated by the digestive juices, especially the parts most posteriorly situated in the stomach. The ratio of 28 stomach items to 186 scat items might be interpreted as indicating that remains are retained in the intestines six times as long as they are held in the stomach, but such a conclusion does not agree with other types of evidence including those provided by snakes kept in captivity. Actually the relative numbers are probably much distorted by changed habits of the snakes that have recently fed. Captive copperheads that had ingested large food items were inclined to be unusually sluggish and spent most of their time coiled beneath any available shelter. Snakes living under natural conditions must have altered their behavior in similar fashion and as a result were less often caught in traps or found in the open. On the basis of experience with captive snakes it is estimated that an average meal would be detectable in the stomach for from three to five days before being reduced completely or passed into the intestine. Digestion does not proceed uniformly in an object reposing in a copperhead's stomach; the more posteriorly situated parts are digested most rapidly. In a mouse swallowed head first the head and forequarters may be completely disintegrated after two or three days, while the hind feet and tail are still intact. If the prey is large, the residues from the anterior portion (normally swallowed first by the snake) may be voided as a scat while the remainder is still being digested. If the prey is small, the scanty residues may be retained in the intestine until the remains of a second meal are added to it completing the formation of a scat.

In only one instance did a copperhead have more than one prey item in its stomach. In this instance the prey consisted of a lactating female vole and three small young of approximately the same size, probably her litter all eaten at the same meal. Of the 381 scats examined six contained nothing recognizable, 215 had only a single item, 52 had two items, seven had three items, and one had five items. Thus nearly 39 per cent of the items in scats were found to be associated with others. Doubtless the true percentage of such multiple occurrences was even greater, but the hair by which mammalian items were usually identified gave no clue as to the number of individuals. Therefore each occurrence of hair was recorded as a single individual, although some such occurrences may have represented two or more animals. The much higher proportion of multiple occurrences in the scats seems to indicate that prey remains are retained considerably longer in the intestines than they are in the stomach. Ordinarily it was possible to count the number of individual animals in a scat only when they were of different kinds, but the chitin of cicadas and other insects was so resistant to digestion that the numbers could be determined readily. Often remains of two or three were associated in the same scat. For the summers of 1958 and 1959 the following figures were obtained:

Total captures of copperheads, 336.

Total prey items from copperheads, 208 (186 from scats and 28 from stomachs, of which 6 were the same).

Total snakes with scats, 157.

Total snakes with stomach items but no scats, 22.

Total snakes with empty digestive tracts, 157.

It is noteworthy that the numbers of snakes with empty digestive tracts and those with scats were exactly equal. However, those still digesting food in the intestines or recently finished probably were less active than those which had fasted and were caught in correspondingly smaller numbers. If this speculation is correct, the proportion of the population having food remains in the intestines at any one time may be considerably more than half. Certainly snakes with food in their stomachs were represented in less than their true proportions, partly because those that had recently fed were less active and less likely to enter traps, and partly because snakes that were trapped usually spent a day or more in the traps before they were found and in many instances may have had time to complete digestion of a meal already in the stomach. Scats may have been lost also by being disintegrated and washed through the quarter-inch wire mesh of the traps in heavy summer rains.

In the winter of 1959-60 two copperheads in the size range of small adults were kept indoors (diurnal maximum temperature 70° F. and nocturnal minimum 53° F. at the place where the cage was located) and were force-fed frequently. To facilitate feeding and avoid injury to the snake, the dead mice that were used as food were skinned back to the level of the hind legs. The skin was left attached to the body but turned inside out so that friction was reduced as the carcass was pushed down the gullet. Digestion was hastened in the early stages by removal of the skin and hair. However under natural conditions food is often digested at a temperature slightly higher and the action is correspondingly more rapid. In the period from December 4 to February 4 one snake was fed five times and the other six times. For from three to five days after feeding the mouse still could be palpated in the stomach. Defecation occurred eight times in each snake. The interval between ingestion and first evacuation averaged 11.4 days (six to 18). There was a tendency for evacuation of the residue from one meal to occur soon after ingestion of a new meal. In four instances a meal was represented by two separate evacuations, the second following two, three, five and nine days after the first. The interval required for complete digestion and evacuation of a meal varied from eight days to 19 days and averaged 13 days. Separate meals averaged 20 per cent of the snake's body weight. The smaller snake ate the equivalent of 120 per cent of its body weight, in six meals; the larger one ate the equivalent of 80 per cent of its body weight in five meals.

Evidence from these feeding experiments indicates that on the average food is retained in the stomach for approximately one-third of the time from ingestion to final evacuation of remaining residues. Were it not for bias introduced in obtaining the snakes by trapping, my sample of 336 captures in summers of 1958 and 1959, yielding 157 snakes with food remains in their intestines, should have yielded nearly 80 snakes with food in their stomachs, but actually there were only 22.

Published reports based on samples of copperheads, obtained by methods other than trapping, all show higher ratios of individuals with food in their digestive tracts than does my own sample. The sample used by Uhler, Cottam and Clarke (1939:610) was collected by crews of workmen in Virginia engaged in such activities as construction of roads and trails. Presumably discovery of snakes by these crews was not dependent on the snakes' activity, but all or nearly all those within the limited areas being cleared or excavated were routed from their shelters, and immediately killed and preserved. Because of these circumstances the collection should give a true ratio of the fed and empty snakes but no distinction was made as to the part of the digestive tract where the prey remains were found. In collections obtained by Surface (1906:189) in Pennsylvania, Clark (1949:258) in Louisiana, and Hamilton and Pollack (1955:2) in Georgia, the techniques of collecting were not described. Conceivably some collecting techniques would yield samples biased in favor of the snakes that were recently fed. Although recently fed copperheads are secretive, they are also sluggish, and once found would be less likely to escape than would unfed individuals.

A feeding cycle averaging approximately 18 days is indicated, with food in the stomach for the first four days, residues in the intestine from the fifth through the thirteenth day, and the digestive tract empty from the 14th through the 18th day. At this rate of feeding, approximately seven meals would be consumed from May 1 to Sep-

TABLE 20. RATIOS OF COPPERHEADS CONTAINING FOOD REMAINS, IN VARIOUS SAMPLES

SAMPLE	Number containing food remains	Total numbers in sample	Percentage containing food
Surface	41	56	73.2
Uhler *et al.*	72	105	68.5
Clark	55	72	76.4
Hamilton and Pollack	13	16	81.4
Total	181	249	72.6

tember 1. In the remaining weeks of activity during autumn I suspect that not more than one meal would be consumed, since the stomachs of most copperheads caught at the rock ledges at that season were empty.

In 297 of the copperheads captured that had food residues in their digestive tracts, weights (exclusive of the food) ranged from 495 grams to eight grams and averaged 118. Weight of prey was calculated to average approximately 22 grams, 18.5 per cent of snake-weight, but individual prey items ranged from less than one per cent to more than 50 per cent of the snake's weight. Taking eight meals in its entire season of activity, an average copperhead would consume 148 grams (approximately ⅓ lb.), amounting to 1¼ times its own body weight. If the food of such an average individual happened to coincide in its composition with that of the population as a whole, it might consist of two voles, two mice, two cicadas and one each of short-tailed shrew, little short-tailed shrew, skink, ring-necked snake, frog and young cotton rat. Actually such a distribution would involve several more meals than the snake probably would take. An individual of average size or above would concentrate on the larger kinds of prey and hence would require fewer separate meals. At a population density of five copperheads per acre—a conservative figure for the Reservation and nearby areas of similar habitat—it is estimated that the copperheads on a square-mile area would annually consume prey totalling more than 1,000 pounds. The effect of this predation on prey populations is difficult to judge. The prairie vole being the favorite prey species, bears the brunt of the copperhead's effect. The annual toll of approximately eight adult voles per acre (or a correspondingly larger number of immature animals) would seem to be a substantial factor in the vole's ecology, but not a decisive one. Where the vole's population density attains a level of 50 per acre, or more, as it often does under favorable conditions, the copperhead's effect would be minor. But where the vole occurs in lower populations of ten to 20 per acre, the copperhead's levy would be felt more, even if the snake were partly diverted to alternate prey species. Other favored prey species including the several kinds of mice, the two kinds of shrews, the five-lined skink, ring-necked snake and the cicada, are all so numerous that the numbers taken annually by the copperhead would amount to only a small part of the annual increase. Rather than controlling their population trends, the copperhead merely exerts some stabilizing influence.

DEFENSE, ESCAPE, AND MORTALITY FACTORS

Defense and Escape

The concealing pattern constitutes the first line of defense against natural enemies; in time of danger a copperhead tends to lie quietly, resorting to defensive behavior only when actually attacked. One lying near a deep crevice may suddenly lunge for shelter when a person approaches, and within two or three seconds may slide down out of sight. In response to a less abrupt or less immediate disturbance, the snake begins to move hesitantly. It then crawls slowly (rate of perhaps two feet per minute) but directly to the nearest shelter. A copperhead that is in a resting coil and is not beside shelter reacts to the approach of a person by a sudden rotation of its head, which is turned to face the danger and cocked upward at an angle of approximately 45°. Without making any other movement than this inconspicuous flick of the head, the snake prepares to strike. A copperhead found in an exposed situation such as a road, sometimes "freezes," or sometimes makes clumsy but vigorous attempts to gain shelter. With its head raised several inches above ground, it progresses by lunging with the anterior part of its body thrown into a loop, in a sidewinder-like type of locomotion. If closely approached, it may strike, lashing out wildly in the direction of its tormentor even though he may be far out of reach. During this performance the snake does not hesitate to move directly toward its enemy, and the lunging movements with which it progresses are not distinct from the strokes with which it threatens or actually attacks.

Vibrating of the tail is a response to severe alarm or disturbance; it was found to be characteristic of copperheads that are cornered, or those that have just been handled. The movement is a spasmodic twitching, resembling that of a typical colubrid snake, and much different from the rapid vibration of a rattlesnake's thick and muscular tail. A pattering or rattling or whirring sound is produced by the vibrating tail, depending on the type of material with which the tail comes in contact. A copperhead that vibrates its tail is thoroughly aroused and ready to strike.

A copperhead that is held down with a stick may not resist or move at all, especially if it has been coiled inactive. If restrained on the posterior part of the body, or the tail, it may merely try to pull away but if the restraint is farther forward the snake may thrash with violent lateral movements, and with jaws widely open, turn its head about in an attempt to bite. It may bite the stick which is used to hold it, or may bite its own body, if in the course of its struggles a coil comes within reach of the gaping jaws. Upon biting itself, the snake releases its grip almost immediately, but is not deterred from repeating the bite as often as its body comes within reach. If grasped by the neck the snake throws its body in a circular loop which is drawn up to a tight kink just behind the point where it is held, at the same time continuing to thrash and squirm vigorously. On one occasion an adult male grasped by the neck with metal tongs, thrashed and twisted so vigorously that vertebrae were dislocated. At intervals a struggling copperhead that is being held emits jets of musk in a fine spray, from the tail glands. Ordinarily the musk is not emitted until the snake is grasped, or otherwise restrained. Then it is released in a jet of fine droplets like the spray from an atomizer. Several such jets may be released, from both sides, in the course of a few minutes while the snake is being handled. Besides the secretion actually sprayed, more oozes from the glands and accumulates at the margins of the anus. It seems that the sole function of the anal glands is defensive, and that their secretion does not serve a social function. Maslin (1950:460) described the females of *A. halys* as having such enlarged postanal glands that their tail-bases were swollen resembling those of the males. In the copperhead, as in other snakes, it is the odor of the skin, not that of the anal glands, that is a stimulus in courtship and serves in the trailing of one individual by another. The musk is of a creamy appearance and consistency. The odor is distinctly disagreeable in high concentrations, but (to me at least) it is far less offensive than the scents of *Thamnophis, Natrix, Elaphe, Coluber* and other common snakes. The musk of copperhead has often been compared to the odor of cucumbers. When a copperhead is handled

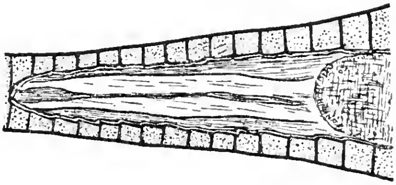

FIG. 24. Ventral view of tail-base of adult female copperhead from which skin and muscle layers have been dissected to expose musk glands. On right is posterior end of cloacal pouch, with ventral wall removed to show opening of duct from each gland.

the vigor of the struggle varies greatly according to the individual and the circumstances; also adult males make a much more spirited defense than adult females. Gravid females are especially docile; when handled they thrash but little, or none at all, and they seldom kink the body in the manner described.

The bite is typically delivered as a short jab, often less than six inches for an adult two to three feet long. Even at such close range the strike may be wildly inaccurate if the snake is highly excited or if the target is moving rapidly. The precision required in timing includes aiming, opening of the mouth, erecting of the fangs and ejection of venom, and is such that the snake may often hit the target with some part of its head without delivering an effective bite. Ordinarily withdrawal from the stroke is instantaneous, but a copperhead that is restrained and enraged may retain its grip for several seconds, straining to embed its fangs more deeply and inject more venom. Occasionally a copperhead that is cornered and is unable to defend itself by striking will react by coiling with its head concealed and protected by part of the body. The hissing of chickadees and titmice disturbed while incubating, has been cited as warning behavior mimicking the hissing of a copperhead (Sibley, 1955:128). However, hissing is not a part of the normal defensive behavior in the copperhead. In fact I have never known a copperhead to hiss audibly under any circumstances, and the sematic behavior which is so characteristic of rattlesnakes is almost lacking in the copperhead.

Natural Enemies and Predation

There are few published records of predation on copperheads. The United States Fish and Wildlife Service's food habits files, containing the records of analyses of contents from thousands of stomachs of common predatory mammals and birds, included no record of a copperhead having been eaten by any animal. In general, potential predators seem to have an instinctive or learned aversion for these venomous snakes.

First-year young are vulnerable to various predators that would not undertake attacking an adult. The mole (*Scalopus aquaticus*) is such a predator. I have often found tunnels of moles beneath flat rocks in the situations where small reptiles are likely to hide, and on the basis of circumstantial evidence, I concluded (Fitch, 1954:133) that, on the Reservation, at least, the mole is a frequent predator on nests of the five-lined skink. In the early summer of 1958 two moles were kept in a large terrarium for more than a month. The bottom of the container was kept covered to a depth of several inches with damp soil. Meat scraps and insects that were offered, were located by scent. The mole tunnelled upward beneath the morsel, and pulled it underground without exposing itself. Several times small reptiles were experimentally introduced into the terrarium. Usually after seeking shelter beneath a flat rock, they were attacked from below by a mole which dragged them underground and ate them. Twice, first-year copperheads were introduced and each time they were promptly attacked, dragged underground and eaten. It seemed that the snakes were unable to turn and strike in the narrow confines of the tunnel before being fatally bitten and immobilized by the mole. When a second-year copperhead was introduced, a mole soon was attracted by the odor or the sound and tunnelled up to it partly emerging. Without touching the snake the mole appeared to sense its larger size and withdrew in panic. Neither mole attacked this snake, although it was left for several days in the terrarium.

The opossum (*Didelphis marsupialis*) takes almost any animal food that is available, and occasionally preys on copperheads, and other such noxious animals that might be avoided by more skilled but warier predators. The opossum's thick, woolly pelage would provide partial protection, especially from small copperheads. However the clumsiness and lack of caution of the opossum might often cause it to be bitten. Such habits perhaps contribute to the short life expectancy of the opossum. Of 79 opossum scats examined on the Reservation in the late summer and fall of 1951, one contained scales of a small copperhead (Fitch and Sandidge, 1953:323), and on at least one other occasion copperhead scales have been noticed in scats that were seen in the field but were not collected for detailed analysis. In November, 1957, partly eaten remains of an adult female copperhead were found, with hairs of an opossum adhering to them, at a rock ledge where many snakes hibernated.

Schlenker (1942:60) described the behavior of two pet house cats that had often caught garter snakes, milk snakes, and other harmless kinds, when they were confronted with a four-foot copperhead, freshly killed and still twitching. One cat, when set on the ground nearby, leaped wildly and yowled in fright, but later regained his courage sufficiently to approach the snake several times and cuff it with a front paw. After each approach he would bound backward several feet to safety. The second cat became tense and nervous as he approached the snake, and stopped short to examine it while still out of range, with his body extended forward to the maximum, ready to bound back at any sign of danger. Possibly the cats' wariness in this instance was occasioned by the relatively large size of this copperhead rather than by any recognition of its venomous qualities, as the article seemed to imply.

The common king snake (*Lampropeltis getulus*) is notorious for ophiphagy and is known to eat pit vipers as well as harmless snakes. Clark (1949:252) reported finding 17 copperheads, along with other prey, in the stomach contents of 301 king snakes (*L. g. holbrooki*) from northwestern Louisiana. Besides the copperheads, there were 27 other venomous snakes represented in the food sample. Minton (1951:322) mentioned finding a black king snake (*L. g. niger*) in a log pile in Floyd County, Indiana, which had a copperhead in its stomach. Six other copperheads were found in the same log pile. Dr. Joseph P. Kennedy (*in litt.*) told of finding a juvenal copperhead in the stomach of a 47-inch king snake (*L. g. holbrooki*) killed on the road near Moss Hill, Liberty County, Texas, on May 1, 1958. The prey had been swallowed head first.

Rattlesnakes have a characteristic and specific defensive behavior with which they respond to the presence of king snakes (Klauber, 1927:13; Cowles, 1938:13; Bogert, 1941:331). Olfactory cues are most important in detection of the ophiphagous enemy. The defense consists of raising the body in a vertical loop which is used to push or strike the enemy, while the rattlesnake presses its head against the ground. On July 6, 1959, a speckled king snake was introduced successively into several different containers where copperheads were kept, and the reactions of the copperheads were noted. The characteristic response described by Klauber, Cowles and Bogert in rattlesnakes was lacking. Nevertheless, the copperheads showed some evidence of recognizing the king snake as an enemy. When the king snake was placed in a container with five young copperheads, the latter at once became alert and wary. They tended to avoid the king snake, and to strike at it whenever it moved within range. One of the young struck another, presumably excited by the sight and/or scent of the king snake. Within a few minutes all the young copperheads were gathered in one corner of the container, facing the king snake and ready to strike. Several times when the copperheads struck at the king snake, the latter jerked back so rapidly that it avoided the stroke, and none of the bites seemed effective. From time to time the king snake tilted its head toward a nearby moving copperhead, as if about to seize it, and sometimes tested the other snake with its tongue, but did not actually attack. Disturbed by recent handling, it vibrated its tail frequently and kept to one corner of the container, obviously on the defensive. The king snake involved in these observations was the only individual found on the Reservation in eleven years of field work. Because of its rarity on this area it cannot be considered an important natural enemy of the copperhead locally.

Minton (1944:462-463) recorded that a milk snake (*Lampropeltis doliata*) overpowered and ate a young copperhead. He also recorded that a captive prairie king snake (*L. calligaster*) ate a small dead copperhead that was offered. Another captive prairie king snake attacked a larger copperhead, but released it and backed away after it had been bitten on the neck.

Keegan (1944:59) described the behavior of a captive indigo snake (*Drymarchon corais couperi*) which, when an adult copperhead was introduced into its container, ". . . seized the prey by the head, and in fact seemed to avoid any other portion of the body. Before swallowing the copperhead, the indigo snake lacerated its head by 'chewing' with lateral movements of the jaws."

Cope (1900:1138) mentioned an instance of a blacksnake (*Coluber constrictor constrictor*) caught near New Haven, Connecticut, which disgorged a well-grown copperhead. Branson (1904:412) recorded an instance of a racer (*C. c. flaviventris*) disgorging a copperhead. Hurter (1911:171) wrote "On May 1, 1898, I caught a Blue-Racer just swallowing a copper-head about two feet long . . . had about half disappeared." Vernon Mann told of finding, near La Cygne, a yellow-bellied racer that was eating a copperhead nearly as big around as itself. This is possibly the same incident referred to by Gloyd (1932:403) as occurring in April of 1929. The "racer had made its capture and was chewing the head and neck of its victim, which was thrashing about in violent efforts to free itself. He [Mann] observed the entire swallowing process, which lasted more than an hour." Mr. Delmer Ferguson of La Cygne also recalled an instance of a large racer found eating a small copperhead.

A large adult female red-sided garter snake (*Thamnophis sirtalis parietalis*) trapped on July 1, 1958, produced a scat in which the only recognizable materials were scales of a small copperhead. This garter snake only occasionally preys on other snakes and certainly is not an important natural enemy of the copperhead.

Pope (1937:99) wrote that no poisonous snakes had been found in the stomach contents of 3,693 hawks of kinds known to prey upon harmless snakes. However, Klauber (1956:1050-1052) has cited many instances of red-tailed hawks preying on rattlesnakes of several different species.

Food habits of the red-tailed hawk were investigated by collecting pellets, chiefly from the ground beneath the nests. Such collections were made on the Reservation in 1952, 1955, 1958 and 1959. In the collections from each nest copperhead remains were represented, and the copperhead was the fourth most frequent kind of prey for the combined sample, with 40 occurrences in 224 pellets or pellet fragments. Because the pellets sometimes were trampled or broken in the nest before falling to the ground, or were broken by striking branches in the fall, the actual number of pellets was probably less than the number actually found. Also, the nestlings, usually two or three in a nest, may have each made more than one meal from the same animal. The number of copperheads actually eaten was hence probably somewhat less than the number of recorded occurrences in pellets. Nevertheless it seems probable that each red-tailed hawk destroys several or many copperheads in the course of a summer, if these snakes are common on its territory. Although the hawk is diurnal and the copperhead is largely nocturnal, their periods of activity overlap after sunset and before sunrise; at these times of day the hawk is unusually active in search of prey. Just how the hawk secures a copperhead with impunity is unknown. Although the stroke of a pit viper is notable for its speed, the reflexes of a hawk are probably even faster. Aside from superior speed, a factor which favors the hawk is its relatively keen eyesight, and the near-sightedness of the snake. Swooping down upon the snake unperceived, the hawk may strike it a fatal blow or may secure a hold on its head or neck, rendering it helpless.

The horned owl is the most abundant large raptor of the Reservation and it might be expected to be an important predator on the copperhead, since the owl and snake are similar in time of activity and in habitat. Several hundred pellets of the horned owl from the area of the Reservation contained no remains of the copperhead. However most of the pellets were collected in the colder half of the year, when the snakes were not active. A horned owl reared in captivity had no instinctive aversion for copperheads or other snakes. On several occasions it was seen to fly down into the outdoor enclosure (open on top) where several were kept, and once lit on the ground and walked within a few inches of two of the snakes. The owl had its attention focused on a cotton rat that had been placed in the enclosure to feed the snakes and gave no indication of noticing the snakes. The copperheads did not respond strongly to the presence of the owl either, but merely drew back their heads in readiness to strike. On a subsequent occasion when the owl was unusually hungry, it flew down into the enclosure and attacked a copperhead. The actual attack was not seen. The snake was carried for a short distance, and struck the owl one or more times high on the medial surface of the thigh. The owl uttered scolding sounds and dropped the snake. Almost immediately the owl showed signs of distress, and ceasing its usual activities perched quietly shifting its position from time to time. After several hours an oozing extravasation was noted, and a small pool of blood had collected where the owl was perched. Approximately eight hours after being bitten the owl suddenly collapsed and died.

Effects of Climatic Extremes

Catastrophic effect of extreme weather conditions on a local population of copperheads was illustrated by my observations in June, 1957, at Independence Creek, Terrell County, Texas. The herpetofauna and habitats of this area in the Stockton Plateau have been described by Milstead, Mecham and McClintock (1950:557). The University of Texas field party which collected in the area in June and July, 1949, found copperheads extremely abundant and obtained 89 during their three-weeks stay. More than twenty were taken in a single night. Nearly all the copperheads found by this field party were found in live-oak groves in the immediate vicinity of Independence Creek (Little Canyon Creek) but a few of those taken overlapped into adjacent habitats.

Encouraged by the account of copperheads in the publication by Milstead *et al.*, and by conversation with Dr. Milstead, I had visited the area hoping to collect a large series of copperheads, but found them to be rare in June, 1957. I talked with many ranchers and other residents of the area. All were familiar with copperheads and agreed that in former years the snakes had been abundant, but that since 1954 they had been rare as the result of a devastating flood. On the night of June 29, 1954, as the aftermath of a hurricane that moved northwest from the Gulf of Mexico, a storm crossed the Stockton Plateau with torrential rain alleged to have totalled more than 20 inches by unofficial observers at several places. In the resulting flash flood Independence Creek overflowed its banks and extended across the valley, about a quarter of a mile wide. Water level rose as much as 20 feet. Many ranch buildings were swept away and several persons were drowned. Locally the live-oak groves were mostly situated on low-lying ground adjacent to the creek, almost entirely within the flooded zone. Many of the trees were undermined by erosion and uprooted (Plate 16, fig 2), or were torn out by the force of the current and transported debris. In situations exposed to the full force of the current almost every tree was uprooted, including many of as much as two feet in trunk diameter. The uprooted trees had been swept downstream for varying distances, and the interlacing tangles of roots on the upstream end of each such tree had collected huge piles of drift. Mr. Charles Chandler, a local rancher and long-time resident, told me that the live-oak groves had been reduced to less than one-third of their former extent by the flood, and his estimate seemed reasonable on the basis of the evidence remaining in 1957.

Presumably most of the copperheads living in the area in 1954 were swept away and drowned in the flood. Some may have survived in the more protected areas by climbing into the live-oaks and keeping above the rising water level. A few may have been near the oak groves but in upland situations that were not flooded. Even though such survivors constituted potential breeding stock to repopulate the remaining oak groves, their habitat was mostly destroyed. The accumulated leaf litter, logs, and dead branches and even the soil had been swept away, leaving bare gravel.

In 1957 there remained at least a dozen oak groves ranging up to a size of more than two acres, along several miles of the lower reaches of Independence Creek. In parts of these areas leaf litter had again accumulated, and habitat conditions appeared to be favorable for the snakes. The root tangles and great piles of debris where there are uprooted trees within the remaining groves or adjacent to them, provide abundant shelter. Of the two copperheads found by me on the night of June 27, 1957, one was climbing two feet high on a pile of driftwood, the other was crawling over leaf litter beneath live-oaks. However, with the advent of improved roads into the area intensive use of the oak groves by humans has become a major factor. In summer, fishermen visit the creek in large numbers. Because shade is at a premium, they concentrate their activities in the groves. The remaining copperheads constitute some hazard to campers. Because of the limited extent of their remaining habitat and its intensive use by humans, it may be anticipated that the snakes will never again regain their former abundance, but will become even scarcer and eventually perhaps will be locally exterminated.

Parasites, Diseases and Injuries

The copperhead has various ectoparasites. Hyland (1950:494) first reported the common chigger (*Trombicula alfreddugèsi*) from copperheads; of six specimens collected in the Duke University Forest, four had chiggers, totalling 260. Most of the copperheads collected on the Reservation in the early years of my study were examined for ectoparasites. Loomis (1956) has reported upon the chiggers. He lists the copperhead as one of 16 important host species (including mammals, snakes, lizards and birds) of the common chigger, locally. This chigger has been recorded from dozens of species of reptiles, mammals and birds, and in fact occurs on most of the terrestrial kinds that are abundant and share its habitat. Because of this lack of specificity the chigger will attach even to humans. Unlike the natural hosts, man does not provide a suitable food source and the attached chigger dies without completing its development, but causes swelling and irritation. Of 107 copperheads examined, 80 carried common chiggers totalling 8,579; 5,898 in July, 1,340 in August, 1,204 in September and 137 in October. Even heavier infestations might have been found in late May or June, but Loomis obtained no samples from those months. A single copperhead may carry several hundred chiggers at one time. The chiggers burrow into the skin between the scales, and often congregate in clusters. The larvae are usually on moist soil in sheltered situations, and they thrive in warm, humid weather. Among the 22 kinds of chiggers occurring on the Reservation, only three others, *Trombicula lipovskyana*, *T. sylvilagi*, and *T. trisetica* were found on copperheads. *T. lipovskyana* occurs chiefly in low, moist meadows having an abundant ground cover of grasses and weeds. Five copperheads from the Reservation had a total of ten of these chiggers, which also have been found on many species of birds, small mammals, snakes, lizards and even frogs and toads. *T. trisetica* has been found chiefly in climax forest of oak-hickory, and has been taken mostly from hosts that are arboreal or semi-arboreal, the gray squirrel, wood rat, white-footed mouse, black rat snake and skinks (*Eumeces laticeps* and *E. fasciatus*). A single specimen was recovered from a copperhead. A single specimen of *T. sylvilagi* was recovered from a copperhead. Larvae of this species usually occur in well shaded places, often about decaying logs, and small mammals are the favorite hosts.

Copperheads that were infested with chiggers showed no ill effects and their infestations were relatively light as compared with those of some other local species, notably the common garter snake, yellow-bellied racer, and black rat snake. However, there is some possibility that occasionally chiggers are the vectors of diseases that afflict snakes.

Various endoparasites inhabit the digestive tract, but insofar as known, none of these is pathogenic. Cloacal smears that were examined microscopically almost always contained large numbers of highly active ciliate protozoans that appeared to be mostly of one species but were not identified. Less frequently microscopic nematodes were found in cloacal smears, but these also were not identified. Crow (1913:123) reported a new species of fluke, *Renifer kansensis,* from the mouth of a copperhead. The material was from Kansas, but no definite locality was mentioned. Flukes of this group require intermediate hosts—a water snail which ingests the eggs and from which free-swimming larvae emerge, and a frog in which a later stage occurs. For the parasite to complete its development, the frog must be eaten by a snake. In the course of my study I examined mouths of several hundred copperheads without finding any flukes in them, although flukes were abundant in the yellow-bellied racers and garter snakes of the Reservation, especially in early summer (Peggy Lou Stewart, "Lung Flukes of *Thamnophis* and *Coluber* in Kansas," an unpublished dissertation on deposit in the library of the University of Kansas). In this connection it is significant that the copperheads of the Reservation rarely prey upon frogs, while the racers and garter snakes do so frequently.

Harwood (1933:66) examined 14 copperheads from the vicinity of Houston, Texas, and found these flukes (*Renifer kansensis*) in two. The species was also found in a pigmy rattlesnake (*Sistrurus miliarius*) from the vicinity of Houston. Hughes, Baker and Dawson (1941:39) listed this same species (as *Neorenifer kansensis*) as a parasite of the copperhead, and also listed *Renifer ancistrodontis,* which Harwood had considered a synonym of *R. kansensis.* Harwood found the diaphanocephalid nematode, *Kalicephalus agkistrodontis,* in stomachs of all of the 14 copperheads, also in the coral snake (*Micrurus fulvius*), hog-nosed snake (*Heterodon platyrhinos*), bull snake (*Pituophis catenifer*), king snake (*Lampropel-*

tis getulus), water snakes (*Natrix sipedon* and *N. rhombifera*) and garter snake (*Thamnophis proximus*). He found the spirurid nematode, *Physaloptera squamatae*, in the stomach of one copperhead, and also in the stomach of a brown skink (*Lygosoma laterale*).

Evidence of disease was noted in copperheads on the Reservation from time to time, but especially in 1951. In the summer of 1951 precipitation was unusually high and temperature was low. Many of the copperheads trapped in autumn had necrotic patches on the ventrals and occasional blisterlike swellings on the dorsal scales. Such individuals often were emaciated, and snakes of other species were similarly affected. There may have been heavy mortality, as in 1952 and 1953, with more traps and greater effort I was able to trap fewer copperheads per season than in 1949, 1950 and 1951.

Otherwise most of the copperheads trapped appeared to be in good condition but occasional individuals showed evidence of injury or disease. Several adult males each had one hemipenis everted, dried and shrivelled. Injury to the tail involving the retractor muscles may have caused eversion in these instances, in which the organ was probably lost eventually. Copperheads rarely had scars of the type common in constricting snakes, that probably are bites inflicted by the struggling prey.

COMPOSITION OF THE POPULATION

The true composition of the population, according to age groups and sex, is obscured because of differences in habits, which, in almost any sample cause certain groups to be represented by too few individuals or too many, in proportion to their true numbers in the natural population. The trends of the figures obtained depend upon the time and place of sampling. There is abundant evidence that in summer the males, especially the old adults, disperse far from the ledges where they are concentrated in autumn, and that the adult females, especially those that are gravid, tend to remain near the ledges. From year to year my samples varied accordingly, with bias toward one or the other group depending on the extent and location of trap lines. Some snakes living far from the ledges where they hibernate, especially adult males, arrive relatively late in the autumn, and in September the population at the ledge is still biased in favor of the adult females. Comparatively few data were obtained in spring, and dispersal begins promptly after emergence from hibernation.

By October 1 the gravid females have nearly all produced their litters, and most copperheads have travelled from their summer ranges back to the rock ledges. Subsequently in all of October and usually the early part of November, the population is concentrated along the ledges, and individuals wander restlessly along the rocks, in search of suitable shelters for hibernation.

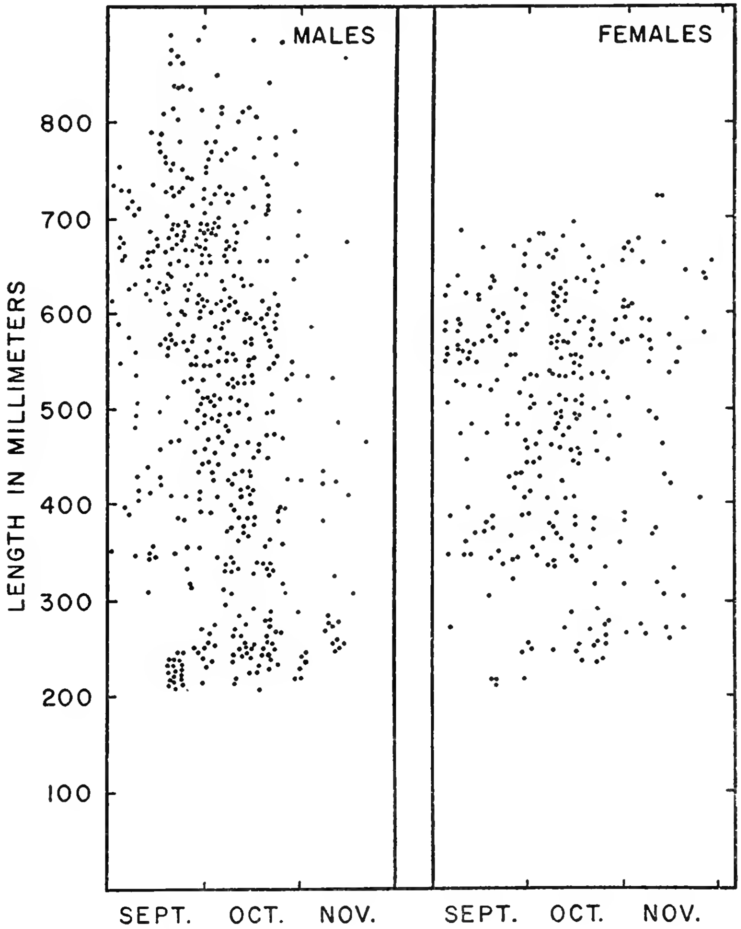

Fig. 25. Lengths (snout-to-vent) in a sample of copperheads caught on area shown in Fig. 1 in autumn. The records almost form a continuum; even the young less than 10 weeks old merge with the one-year-olds.

I consider this autumn sample by far the most suitable for indicating the composition of the population, and therefore have used it exclusively. In the eleven seasons of field work a total of 637 copperheads were recorded in October and November. Actually the number of individual snakes represented was somewhat fewer because the same individual might be recorded in two or more years, each time in a different age group.

Actual age was known for relatively few of the snakes, namely for those that had been marked early in life. However, each was assigned to a probable age group. Since birth occurs in early autumn, this October-November sample consisted of discrete annual age-groups with no intermediates. A male of 620 mm. in snout-vent length, for example, was assigned to the four-year-old class on the basis of typical growth rates, although there was some chance that he might be an oversized three-year-old or an undersized five-year-old. Arbitrary size limits were assigned to each supposed age-class. Although extensive overlap in size is known to occur in snakes of different age classes, it is assumed that these are reciprocal and largely cancel out each other, so that the number of snakes in the size range most typical of three-year-olds actually reflects the approximate relative numbers of three-year-olds, despite the fact that some of them are two-year-olds and four-year-olds. For the recently born young of the year and for the one-year-olds there is little likelihood of individuals being assigned to the wrong age group. But in the older snakes there is increasing overlap in size. Assignment of a large adult to any specific age group, on the basis of size, is more likely than not to be erroneous. The size

TABLE 21. NUMBERS OF COPPERHEADS OF VARIOUS SIZE GROUPS, REPRESENTING ANNUAL AGE GROUPS, IN AN AUTUMN SAMPLE OF 637 RECORDS

AGE IN YEARS	Males		Females		Number of both sexes combined
	Size-range in mm.	Number of snakes	Size-range in mm.	Number of snakes	
0 (newborn)	200–299	91	200–299	35	126
1	300–409	54	300–390	33	87
2	410–530	85	391–510	51	136
3	531–589	52	511–565	33	85
4	590–650	39	566–589	24	63
5	651–684	29	590–615	17	46
6	685–734	24	616–635	10	34
7	735–785	21	636–650	5	26
8 or more	786 or more	17	651 or more	17	34

range arbitrarily assigned to each age group, and the numbers of snakes of each sex in the total sample of 637 are shown in Table 21.

Even these figures are biased in some respects by differential habits of the snakes, and do not represent the true composition of the population. The juvenal snakes are surely represented in less than their actual numbers. Newborn, and also one-year-olds, must outnumber two-year-olds but more of the last were obtained. Traps in which most of the snakes were obtained may somehow be selective, catching a higher proportion of the adults present than of the young. Small copperheads may avoid traps more easily by squeezing behind or beneath them, because they are able to pass through smaller openings. Or the small snakes may merely travel less. Their comparatively small bulk would permit them to utilize relatively small fissures and interstices in the rock outcrops, whereas large snakes would less readily find hibernacula of sufficient size to accommodate them and would require longer search. Regardless of the availability of shelter, distance traveled may be in a general way, proportional to the size of the snake; for a foot-long individual the time and effort required to travel one foot might be approximately the equivalent of a three-foot movement in a snake three feet long.

Of the 637 copperheads in the autumn sample, 288 were allocated as three-year-olds or as snakes of older groups, all sexually mature and past the period of most rapid growth. Of the 288 mature snakes, 106 were females. Presumably at least half of these sexually mature females had produced litters of young in the period of ten weeks preceding their captures; with the average litter 5.25 young, the 53 breeding females would have produced a total of 278 young. If females all breed for the first time in their third years and breed in alternate years thereafter, the breeding population would amount to more than half of the adults because three-year-olds are more abundant than any older age group. Of the 106 adult females actually recorded, 63 were tentatively classed as odd-year individuals (3, 5, 7, 9, 11 or 13 years old), and if all these produced average litters of 5.25 young, the annual brood would amount to 330. However, some three-year-olds, those that lag in their development and remain undersized, fail to mature sexually and fail to ovulate, and it seems safer to assume that approximately half the adult females breed annually in this locality. Only 126 recently born young were actually captured in the sample, indicating that more than half those that should have been caught were missing from the sample.

The annual brood of 278 young calculated to have been produced by the 288 adult snakes might be expected to sustain losses in the subsequent three years sufficient to reduce it to 85, the number of three-year-olds. If this reduction occurred at a constant rate, an annual loss of 33 per cent would be indicated, with reduction to 186 one-year-olds and 125 two-year-olds. The number of two-year-olds actually obtained was 141, suggesting that the two-year-olds are fully as well represented in the trap sample as are the older snakes.

At a somewhat slower rate of loss in the adults, 29 per cent annually, four-, five-, six- and seven-year-olds would be represented by 69, 49, 35 and 25 individuals respectively. These figures correspond remarkably well with the numbers actually caught—85 (three-year-olds), 63, 46, 34 and 26. If the same rate of loss were continued in subsequent years, the numbers would be reduced to one or two in the fourteen-year-olds, and obviously snakes of greater age would be rare. The oldest known copperhead detected in my study, for which a fairly definite age could be established, was a fourteen-year-old and several twelve- and thirteen-year-olds were also recorded. Thus, an assumed annual loss of approximately 33 per cent in young up to an age of three years, and of 29 per cent subsequently fits best with the available data, although it might be expected that the rate of loss would change continually at different stages in the life cycle. For example, young of the year would appear to be much more vulnerable to predators than large adults.

Of the 126 young of the year in my sample, 12 were not sexed and the remaining 114 included 84 males and 30 females. The 2.8 to 1 sex ratio in this sample approximates the ratio obtained from young born in captivity. In the older age groups, combined, females comprise approximately 39 per cent of the sample. Hence it seems that the heavy preponderance of males in the newborn snakes is in part compensated for by greater mortality in the males, especially in their first year of life. It is not evident why the young males should be subject to heavier mortality than the young females.

Recaptured, marked copperheads of known age are available in fairly substantial numbers to permit tracing of growth up to an age of seven years. Beyond this age the records are relatively few and their evidence is somewhat conflicting. For eight males known to be seven years old, length ranged from 709 to 791 mm. and averaged 744. Of 13 males known to be more than seven years old,

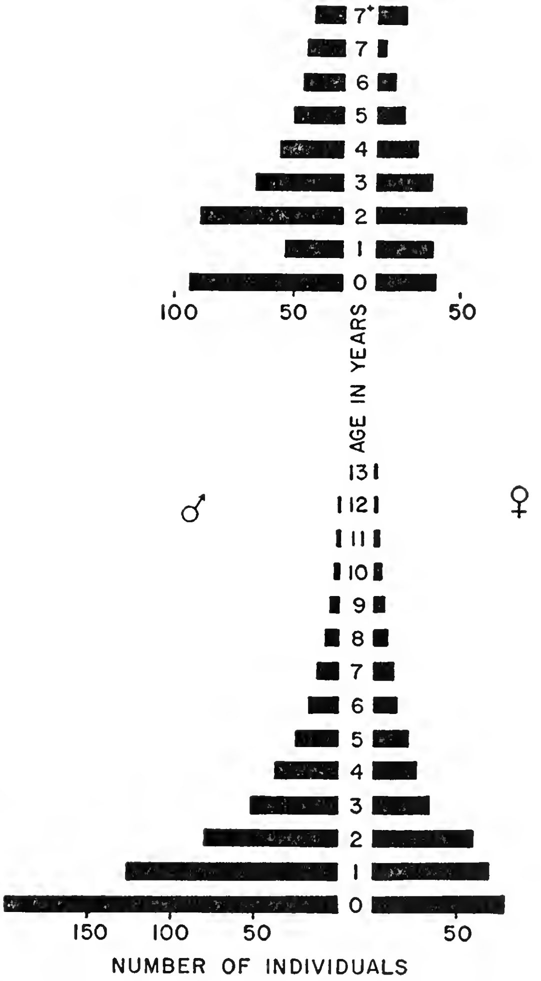

FIG. 26. "Age-pyramids" for the copperhead on the University of Kansas Natural History Reservation and Rockefeller Experimental Tract. The upper figure shows distribution in the actual sample; the lower figure is hypothetical, showing the probable age-distribution in the natural population, but any sample collected is more or less biased because of differential habits in the sexes, and in young and adults.

one had a length of 733, another 783, and the remaining eleven all exceeded 800. A length of approximately 775 mm. may therefore be established as the dividing line between those seven years old or less and those eight years old or more. Similarly, in females an upper limit of 650 mm. was established for seven-year-olds. Of the 637 snakes in the fall sample (actually representing a population of 902, with the missing young), 34 were adults exceeding seven-year-old size, and these 34 were equally divided between the sexes, 17 males and 17 females. Assuming that in these large, old adults the same rate of loss continued (approximately 29 per cent annually) that had prevailed in each of the three preceding years, the original brood of 292 young would be reduced to a single survivor in the fifteenth year.

Perkins (1955:262), Conant and Hudson (1949:8) and Shaw (1959:337) have published many records of the longevity of captive snakes including copperheads. Individuals of two subspecies of copperheads have attained ages slightly exceeding eighteen years in zoos. Once adjusted to captivity, snakes in zoos have an excellent opportunity to live out their potential life span free to a large extent from the usual hazards of predation, disease, parasitism and extremes of weather which account for most of the mortality in natural populations. I suspect that in the wild, attainment of an age of 18 years is exceedingly rare.

NUMBERS

For snakes in general, the published literature concerning population densities is meager, and impressions are liable to be erroneous. However reliable information concerning numbers is necessary for any appraisal of the species' economic or ecologic role. Because of the copperhead's secretive habits, no precise measurement of the population on any area was possible. It is certain that population densities differ greatly on neighboring areas, depending on their suitability as habitat, and also that numbers normally fluctuate somewhat from year to year on any area, although, of course, changes are much less rapid than in some other small vertebrates which have a higher reproductive potential.

There are no definite published statements concerning population densities of the copperhead. Most authors have used rather vague terms, such as "common" or "scarce," but others have mentioned the number encountered in a season or in a single day. Excluding aggregations found at hibernation "dens," the greatest concentration has been reported by Guidry (1953:55) who captured 35 in a small area within a few hours, in southeastern Texas. Milstead, Mecham and McClintock (1950:557) found a comparable concentration near the Pecos River in western Texas and noted that because of their abundance the snakes constituted a hazard to campers and livestock. On a small island off the west coast of Manchuria, Koba (1938:247) found the Palearctic pit viper (*Agkistrodon halys*) to be extraordinarily abundant, and he estimated that in the south part of the island the population density amounted to almost one snake per square meter. These snakes were feeding upon migratory birds. Doubtless the high concentration was made possible by peculiarities of the insular habitat, with an abundant food supply renewed from outside the ecosystem. Although the copperhead attains no such concentrations, this instance is of unusual interest in demonstrating that snakes may attain remarkably high densities under optimum habitat conditions.

One clue to population density in the copperhead is the number actually collected on a sample area, at a time when the snakes are dispersed on their summer ranges. The area most intensively sampled by me was the small valley where the Reservation headquarters are located. Excluding surrounding wooded areas, cultivated fields to the west beyond the Reservation boundary, and a formerly cultivated field on the Reservation, this valley comprises a block of 25 acres, approximately 2,000 feet long, and 1,000 feet in greatest width near the middle, but narrowing at each end. In the summer of 1958, 66 copperheads were caught on this area. Although the area in question was completely surrounded by less favorable habitat, each copperhead caught on the 25 acres probably had a home range extending onto adjacent areas. Addition of a peripheral strip of the radius of a typical home range would greatly increase the sampled area and if it could be assumed that all snakes present were found, the population represented would be less than one per acre. Actually the 66 copperheads captured must represent only a small minority of those present on the area in 1958, because, up until the end of the summer, and in the following year, new snakes continued to be better represented than the old ones among those captured.

Interpretation of the data bearing on population density must take into account the vagility of the snakes, and the differences in this regard between individuals of different ages, sexes, and stages of breeding cycle. Also it must take into account the rate of population turnover as indicated by known mortality and natality. Because of the copperhead's secretive and elusive habits, a long time is required to collect a sufficient number on any area for a census computation, and within such an interval there is sure to be some change in the population. Shifts in home range and movements within a range cannot be distinguished with certainty in the data now available. Until such distinction can be made, the rate of mixing of populations between a sampled area and adjacent areas cannot be judged, and an unknown error is introduced into any census computation. Obviously, the shorter the time involved in sampling and the larger the area, the less important will be the error introduced by the mixing of populations. Also, in a census computation based upon the ratios of recaptured individuals to others, mortality in the animals marked and their replacement by other unmarked individuals has to be taken into account. When mortality has occurred, an erroneously low ratio of marked individuals in the sample and an erroneously high population figure may result. However, in the copperheads the marking and handling entailed no appreciable mortality, and it seems safe to assume that mortality rates were similar in the marked snakes and those that were unmarked, approaching 30 per cent annually in both groups. The young are all born at approximately the same time of year and in their first year most are recognizable as a size group, hence are not included in the samples from which the ratios of marked individuals to others are derived.

The so-called "Lincoln Index" has been widely used in censusing of birds and mammals. Also, under a different name, it has been applied to populations of fish, and to a lesser extent has been used on populations of amphibians and reptiles. The technique of censusing involves two distinct periods of sampling, which preferably should be short and close together. In the first period a substantial number of animals on the selected area are recognizably marked, and in the second period a sample is obtained that includes some of these same marked animals and demonstrates their relative abundance as compared with the remainder of the population. For example, if 100 individuals were marked in the first period, and in the second period another lot of 100 were obtained, including ten of the same individuals in the original lot, the ten to one ratio would indicate a total population of 1,000 in the area sampled. The assumptions are implicit, that: (1) sampling is random, covering the entire area uniformly and favoring neither the marked nor the new individuals, and (2) the population does not change within the periods of sampling nor between them. Actually these conditions are rarely satisfied, and census figures obtained by the method are usually more or less distorted. Whether the census yields fairly accurate information concerning the animal's abundance or creates highly erroneous impressions regarding it depends upon the quantity and quality of the data obtained and upon the judiciousness with which they are used. Various correction factors have been introduced into the formula of the Lincoln Index by different workers, making it complex in some instances, but unfortunately the distorting factors usually cannot be measured readily.

Sixteen different census computations, based on the Lincoln Index, have been made of the population of copperheads on parts of the Reservation. These figures vary over a wide range. To some extent they may reflect the differences in population density that occurred from time to time and from place to place. But it is believed that the differences result chiefly from samples that are biased by various immeasurable sources of error, and are too small anyhow to yield highly accurate figures. Even though no one census figure can be considered accurate, the *trends* of the figures are considered significant. Also, the trends provide some basis for judging the extent of error introduced by such variables as the time factor. Composite censuses based on several samples taken under similar conditions are deemed more reliable than a census from any one of the component sets of figures.

The 1,532 copperheads obtained on the Reservation and adjacent areas in the course of my study were distributed over eleven seasons and represent several generations. Therefore the total indicates little concerning the numbers present at any one time. In 1958 and 1959, the last two seasons of field work when operations were most concentrated, a total of 616 was obtained. These were not all contemporaneous on the area, of course, as two successive annual broods of young were born within the seventeen-month span of the two seasons' collecting. However, the young-of-the-year that were obtained comprised only a small minority of the total sample. The normal wandering of individuals within a seventeen-months period would result in some loss of the original population, with compensatory gains from immigrants. However most individuals are believed to retain small home ranges over periods of years, with regular seasonal movements to and from hibernation shelters. Therefore, notwithstanding some replacement through mortality, reproduction, and migration, a substantial majority of the 616 snakes must have been actually contemporaneous on the area.

The area represented by the 616 copperheads caught in 1958 and 1959 cannot be definitely determined. Actually two populations, broadly overlapping, but not identical, were represented. Those caught along rock ledges in fall had gathered from various distances and directions, some from within the areas trapped in summer, and some from outside areas. Likewise, the snakes trapped in summer, in field or meadow habitat, had moved there from rock ledges at various distances and directions, some within the areas of operation in the fall trapping, and some outside these areas. The area sampled was hence substantially larger than that over which the traps were actually dispersed, but was probably somewhat less than a square mile. A block of nearly 200 acres in the southern and eastern parts of the Reservation was not trapped. A minimum population density in the neighborhood of one copperhead per acre seems to be indicated by these data.

The extent to which the actual population of the areas is represented by the 616 snakes captured in the two seasons may best be judged by the ratio of new individuals to those previously captured in the final weeks of field work. In October and November, 1959, 97 individuals were caught, and only 18 of these were snakes caught previously in 1959, or in 1958. Even if young of the year are excluded from the counts, the newly captured individuals exceed those previously captured in a ratio of more than four to one (73 to 17), indicating a population of 2,222 copperheads on the area of the study. If it is assumed that by October, 1959, 30 per cent of the snakes captured and released in the preceding 15 months were already eliminated through natural causes, the 17 individuals recaptured would represent an original 243 individuals, and the Lincoln Index would indicate a total population of 1,725—a population density of 2.7 per acre, if it is assumed that the area represented is exactly a square mile. This figure is probably low since the figures apply primarily to adults and well-grown young. First-year and second-year young, which must be relatively abundant, are so poorly represented in all samples that it is estimated approximately 30 per cent of the population is overlooked. At the time of the annual maximum, in autumn, the figures obtained may represent a population of 2,450—3.6 per acre.

An unbroken sequence of 11 consecutive seasons' records was obtained from trapping in autumn along the hilltop ledges. In general the stretches of ledge where traps were set, and the specific trap sites corresponded from year to year. However, operations were gradually expanded; more traps and larger traps were utilized. Also, stretches of ledge which were relatively unproductive in one year were often abandoned the following year. Such lack of correspondence between consecutive samples would tend to result in a too low ratio of recaptures (assuming that each snake returns to its original hibernaculum) and an erroneously high census figure. Further shortcomings are the year-long intervals between successive samples, and the concentration of traps along certain stretches of ledge, with extensive intervening unsampled areas. Obviously the samples are inadequately small, as in four different years no recaptures from the previous season were made, while in each of three other years the census was based upon a single individual recaptured.

Table 22 shows the samples obtained for each year, and the resulting census figures obtained by the Lincoln Index.

TABLE 22. NUMBERS OF CAPTURES EACH AUTUMN, AND OF RECAPTURES FROM THE PRECEDING AUTUMN, MADE ALONG THE LEDGES WHERE THE COPPERHEADS HIBERNATE, SERVING AS A BASIS FOR "LINCOLN INDEX" CENSUSES OF THE POPULATION

YEAR	Number in original sample	Number in following year's sample (exclusive of young)	Number occurring in both samples	Total population estimated
1949	26	32	0	....
1950	49	49	0	....
1951	71	15	0	....
1952	35	18	2	315
1953	34	27	1	919
1954	72	32	3	768
1955	38	27	1	1027
1956	39	28	1	1000
1957	32	86	0	....
1958	97	57	3	1824
All ten combined	492	372	11	1664

The composite census from all ten samples, indicating a population of 1,664, is probably more reliable than the figure from any one of the separate annual censuses. Normal loss of marked individuals and their replacement by younger snakes would reduce this figure by some 30 per cent, but this would be compensated by an addition of 30 per cent to allow for the segment of the population (younger snakes) not represented in the sample. The population density indicated for the 218-acre area is 7.6 per acre. This figure may be somewhat high because of lack of precise correspondence of successive samples.

Another series of three censuses was each based upon: (*a*) a preliminary sample obtained along the ledges in autumn, and (*b*) a follow-up sample obtained in the valley the following summer. These censuses and a composite derived from them are shown in Table 23.

TABLE 23. NUMBERS OF CAPTURES IN AUTUMN ALONG LEDGES WHERE COPPERHEADS HIBERNATE, AND IN FIELDS IN THE FOLLOWING SUMMERS, SERVING AS A BASIS FOR "LINCOLN INDEXES" OF THE POPULATION

YEAR	Number in original sample	Number in following summer's sample (exclusive of young)	Number occurring in both samples	Total population estimated
1956................	39	44	2	858
1957................	33	106	1	3498
1958................	97	109	3	3497
All three combined....	169	259	6	2430

In this instance also, the composite census is probably the most reliable. The computed population of 2,430 snakes seems excessively high. Non-correspondence between the population at the ledge in autumn and that in the valley in summer probably results in an erroneously low ratio of recaptured snakes. In any case the figure should be reduced by perhaps 15 per cent to allow for normal mortality of the marked snakes in the period of months intervening between samples but should be raised by 30 per cent to allow for the younger snakes not represented in the samples. An adjusted figure of 2,950 is indicated representing a population density of 13.6 per acre.

Still another set of censuses were each based upon: (*a*) a preliminary sample obtained in the valley in summer, and (*b*) a follow-up sample obtained at the hilltop ledges in autumn of the same

TABLE 24. NUMBERS OF CAPTURES IN SUMMER IN FIELDS, AND IN AUTUMN OF THE SAME YEARS, ALONG LEDGES, SERVING AS A BASIS FOR "LINCOLN INDEX" CENSUSES

YEAR	Number recorded in summer sample	Number in autumn sample (exclusive of young)	Number occurring in both samples	Total population estimated
1957................	44	28	0	....
1958................	106	88	3	3109
1959................	109	56	6	1025
All three combined....	259	172	9	2455

year. In 1957, when both samples were small, no recaptures were made in fall, so census computations were possible only for 1958 and 1959, as shown in Table 24.

Like the fall-to-summer census figures, the summer-to-fall figure needs to be adjusted by subtraction of perhaps 15 per cent, to compensate for normal loss and replacement of the marked snakes, and addition of 30 per cent to allow for unrepresented young. In this instance also, the population density indicated is approximately 13.6 per acre.

The remaining censuses all are based on samples collected in summer in the valley and in several hilltop fields. These areas were sampled adequately only in 1957, 1958 and 1959; and in 1957 the samples were relatively small. Table 25 shows the two censuses derived from the consecutive annual samples, and the composite figure derived from them.

TABLE 25. NUMBERS OF CAPTURES IN SUMMERS OF THREE CONSECUTIVE YEARS, IN FIELDS, SERVING AS A BASIS FOR A "LINCOLN INDEX" CENSUS

YEAR	Number in original sample	Number in following year's sample (exclusive of young)	Number occurring in both samples	Total population estimated
1957................	44	101	3	1481
1958................	101	85	4	2146
Both years combined	145	186	7	1927

For the composite census figure obtained of 1,927 snakes, reduction of 30 per cent to compensate for the normal loss and replacement of the marked snakes in the annual cycles and increase by 30 per cent to allow for young unrepresented in the sample, cancel each other. Several disjunct fields were included, and the total area represented by the snakes caught is uncertain, but probably somewhat less than the 218 acres that includes both these fields and the hibernation ledges. If it is assumed that the entire 218-acre area is represented, a population density of 8.8 per acre is indicated.

A final series of census figures was obtained by dividing each summer (1957, 1958, 1959) into two sampling periods, late April-May-June and July-August, respectively. In 1957 samples were relatively small and no recaptures were made in the late summer period. The census figures obtained for 1958 and 1959, and the composite from them are shown in Table 26 and apply to the same 25-acre area mentioned earlier, the valley on the west side of the Reservation, where the headquarters are located.

TABLE 26. NUMBERS OF CAPTURES IN SUMMER SAMPLES OF THREE DIFFERENT YEARS, IN A 25-ACRE VALLEY. FOR THE PURPOSE OF SAMPLING, EACH SUMMER IS DIVIDED INTO AN EARLY PERIOD, APRIL-MAY-JUNE, AND A LATE PERIOD, JULY-AUGUST, THE NUMBERS OF COPPERHEADS CAUGHT IN BOTH EARLY AND LATE PERIOD SERVING AS A BASIS FOR A "LINCOLN INDEX" CENSUS

YEAR	Number in original sample	Number in following sample	Number in both samples	Total population estimated
1957	11	12	0	....
1958	32	37	3	393
1959	17	17	1	289
All three combined	60	66	4	330

Since most captures were made in late May, June, and July, the interval between the two samplings involved in a census averaged only a few weeks, and perhaps no adjustment of the figure, to allow for the normal mortality of marked snakes, is necessary. The composite census figure of 330 snakes represents a population density of 13.2 per acre, if it is assumed that all caught were limited to the 25-acre block where they were trapped. It seems more reasonable to assume that they ranged freely over adjacent woodlands. If this assumption is correct, a peripheral strip equal in width to the radius of a typical home range (581 feet for males and 381 feet for females) would need to be added, and I estimate that this would increase the area represented to 113 acres for males and 72 acres for females. With a separate census computation for each sex to allow for the difference in area represented, a figure of 3.7 copperheads per acre is obtained. However, if allowance is made for the 30 per cent of the population (of younger age group) not represented in the samples, a population density of 5.3 per acre is indicated. This census is more satisfactory than most of those in the foregoing series because (*a*) intervals between sampling periods, and the periods themselves, are relatively short; (*b*) snakes are dispersed and sampling is well randomized; (*c*) the two samplings of each census correspond almost exactly in area covered.

The population density indicated by the several sets of censuses varies from a minimum of 3.6 to a maximum of 13.6, but the higher figures are probably distorted by non-correspondence between the two samplings of each census giving an erroneously low return of marked snakes, and the lower figures are perhaps equally far off the mark because of overestimation of the several areas involved, or other sources of error. Although no highly accurate census is feasible, the population density on the Reservation probably usually averages between five and seven per acre, in summer somewhat higher than this in the brushy fields, which are the snakes' preferred habitat, and somewhat less in woodlands. In autumn the population density is much higher than seven per acre in the hilltop edge areas where the snakes gather to hibernate.

By a process of extrapolation, from the census data obtained from the Reservation, and from the relative abundance of copperheads there and elsewhere, as judged from the results of hunting them without the use of traps, I conclude that in Douglas County and adjoining counties a population of five per acre is fairly typical where favorable habitat exists, on rocky wooded hillsides with adjacent grassland and brush, and that in this same area, in various localities where habitat conditions approach the optimum, populations of ten to 20 per acre occur.

RELATION TO MAN

Attitudes of the Public

Since the time of the early colonists the copperhead has been well known to Americans, and in the United States it is the one species of venomous snake most frequently encountered by the public. Wright (1950) and Wright and Wright (1957) have listed the following vernacular names applied locally to the copperhead: beech leaf snake, chunkhead, copper adder, copper-bell snake, copper belly snake, copperhead moccasin, copperhead viper, copper snake, copper viper, cottonmouth, deaf adder, deaf snake, death adder, dumb rattlesnake, dumb snake, harlequin snake, hazel-head, highland moccasin, *kupper schlange,* lowland moccasin, moccasin, pilot snake, poplar leaf, rattlesnake mate, rattlesnake pilot, red adder, red eye, red oak snake, red snake, red viper, rusty moccasin, sand viper, thunder snake, upland moccasin, viper, white oak snake. Many of these names were originally listed by Rafinesque (1819:84) as used for the species in New York State.

Some of the names listed above are based upon folklore prevalent in pioneer times, and perhaps adopted from earlier aboriginal versions. A widespread superstition pertained to the "piloting" of the rattlesnake by certain other snakes—most notably the copperhead and the "pilot" black snake (*Elaphe obsoleta*). Klauber (1956: 1243) cited an early account by the Count de Crèvecoeur in 1782 stating that the copperhead is called rattlesnake pilot because it comes out of hibernation a week earlier than the rattlesnake, and always precedes it in crawling about. Milling (1937:43) mentioned a belief, widely held in the southeastern states, that if a copperhead was killed it was necessary only to watch the body for a sufficient length of time, and a rattlesnake, following behind would appear and could be slain also. The copperhead was believed to be the female of the rattlesnake. Strecker (1925:49) wrote of an old Texas bottomland myth to the effect that the copperhead leads the rattlesnake to its prey. Beck (1952:143) mentioned various beliefs of the backwoods people of the Blue Ridge region in the Appalachians, concerning snakes. The copperhead is one of the eight kinds of local snakes (some of which are legendary, like the hoop snake) known to these people, although many species of snakes actually occur in the Blue Ridge region.

Elsewhere the copperhead is often confused with various harmless snakes, especially the hog-nosed snake (*Heterodon platyrhinos*) and the milk snake (*Lampropeltis doliata*). The average person, especially a suburbanite or city dweller, recognizes few kinds of snakes with certainty, and is inclined to regard all kinds as dangerous until he has definite evidence to the contrary. This attitude probably prevents some accidents, but unfortunately it results in the needless killing of many non-venomous and economically beneficial snakes. In extensive areas of the Midwest and Northeast, the presence of the copperhead is the basis for this uncertainty, since the easily recognized rattlesnake is the only other type of venomous snake found. An elderly farmer who owned land adjoining the Reservation, and had lived most of his life in the same neighborhood, told me, when asked, that he did not know whether there were any copperheads on his farm. He did not recognize them, or any other snakes except for rattlesnakes. His attitude was fairly typical of that of many local farmers, to whom "a snake is a snake" to be killed on sight, and most kinds of wildlife are regarded as "varmints."

Throughout most of the area it inhabits, the copperhead is, in varying degrees, hated and feared. Although, of course, attitudes toward snakes differ greatly among different persons in the same community, the copperhead is, in general, accepted rather casually. Compared with any of the several species of rattlesnakes that share its range, it occasions little alarm; its smaller size, more retiring habits, and lack of the rattle cause it to be less feared. Although it is usually killed on sight, as a matter of course, concerted efforts rarely are made to reduce its numbers locally.

In the one exceptional instance known to me in which copperheads were purposely hunted and killed, at Trading Post, Kansas, in 1958 and 1959, the motivation seemed to be not so much the local extermination of the snakes as the competitive sport of killing them in large numbers where they were exceptionally abundant. The method of hunting consisted of driving at night over a certain stretch of road where the snakes were abundant. Those caught in the glare of the headlights usually "froze" to immobility and could be clubbed without serious risk to the hunters.

In localities where copperheads are scarce they are more feared. Persons in suburban communities, who lack first-hand familiarity with snakes, and know the copperhead only by its fearsome reputation, are those most affected. Oliver (1958:46) stated: "It is no exaggeration to say that there are thousands of people around the New York area alone who are terrified by the possibility of an encounter with a Copperhead. Last year I was consulted by two different persons who were considering selling their homes because of reports of Copperheads on their property. One lived in a section where no Copperheads had been found in twenty years, but a large milk snake was killed in her yard by a policeman who said it was a Copperhead."

Occasionally landowners have found the presence of the copperhead an asset, and have been able to capitalize on the popular dread of snakes to prevent trespassing and vandalism. Oliver (1958: 40, 41) mentions instances in which signs have been posted reading "Beware of Copperheads," or "Do not feed or annoy the Copperheads," which were effective in discouraging the public.

Dread of the copperhead is not a major factor in the lives of the people who live in the areas where it abounds. In this respect, it contrasts with several species of the larger rattlesnakes, which frequently cause human deaths, and which are so greatly feared that their presence influences, to some degree, the habits and outlook of the people locally. Schmidt (1945:31) has written of the social prestige gained in the community (formerly, at least) by the victim as the result of a rattlesnake bite, in the back-country of the Edwards Plateau in Texas. Furthermore, in certain parts of the country, the killing of a rattlesnake is generally regarded as a feat establishing the valor and virility of the slayer. Such incidents are often the subjects of long and boastful accounts, in which the size, aggressiveness and proximity of the rattlesnake, are highly exaggerated. In contrast, the killing of a copperhead seems to confer little, if any, prestige, and is not likely to be talked of more than the killing of a non-poisonous snake. It is a curious fact that various harmless snakes, notably the racer (*Coluber constrictor*) are feared by rural people as much as the copperhead, and are widely credited with being venomous. The rapid, and sometimes aggressive, movements of a racer often cause panic, while the secretive and sluggish copperhead causes less excitement when it is encountered.

The circumstances under which copperhead bites are sustained often illustrate complete lack of caution or failure to comprehend and avoid the danger, on the part of the persons who are bitten. Bites are often inflicted on the bare feet or ankles, and often the victims are walking in the dark in places where the snakes might be expected to roam. I refer here to *bona fide* accidents happening under natural conditions, to persons unaware of the presence of snakes until the bites were inflicted. However, many other bites are sustained by persons catching or handling copperheads. There are probably hundreds of persons in eastern Kansas and western Missouri who have handled live copperheads. Boy Scouts and high-school biology students for instance frequently hunt and catch them as a part of group activities out-of-doors. These inexperienced persons often grasp, handle, and release copperheads in such a manner that the snakes are able to bite.

My work with copperheads on the Reservation generated widespread uneasiness and even hostility in nearby communities. The practice of marking and releasing snakes, especially, was looked upon with disfavor and was blamed for alleged alarming increases in the numbers of copperheads in the same county or those adjoining. Farmers on land adjacent to the Reservation were urged by me to save any copperheads killed, so that these could be examined, but none of the snakes was ever offered. Absurd rumors such as one that thousands of poisonous snakes had been brought from elsewhere and released on the Reservation, were seized upon by the local press for their sensational appeal, and as a result gained credence among many of the less well-informed country people.

Survival Under Modern Conditions

Early in this century Morse (1904:137) wrote that the copperhead in Ohio ". . . is not common as formerly and is undergoing certain extermination." Although the copperhead and most other forms of wildlife have been eliminated from many areas owing to cultivation or urbanization of the land, Morse's prediction is still far from fulfillment. Indeed the species has actually been favored by some of the changes brought about by man and its populations have increased in certain areas. Secretiveness, nocturnality, cryptic coloration, and a fairly wide choice of prey species are factors that have favored survival under altered conditions and in association with medium to dense populations of man. Also a relatively small individual home range probably is an important factor, as any snake that attempts to cross a thoroughfare with heavy motor traffic is usually doomed. Atkinson (1901:152) wrote that in Allegheny County, Pennsylvania, the copperhead remained fairly common in some localities for many years after both the timber rattlesnake and the massasauga had become extinct, surviving because of retiring disposition and effectively concealing pattern. Five years later Surface (1906:187) wrote that in the same state it had become extinct in most cultivated districts and that it was being gradually reduced in the wilder, mountainous parts. In the same year Stone (1906:167) observed that the copperhead was becoming scarce in thickly settled districts, such as those of York and Fulton counties, Pennsylvania. Ditmars (1935:23) wrote that the species was increasing in abundance along the Delaware River, and still occurred along the Palisades of the Hudson River, although the timber rattlesnake had been exterminated there nearly fifty years earlier. Strecker (1935:26) wrote that in McLennan County, Texas, the copperhead had become much less abundant than formerly, but that it was better able to withstand encroaching civilization than were some other kinds of snakes, because of its timid disposition and lurking habits. He explained that formerly when large rotting logs were abundant in the bottomlands of the Bosque and Brazos rivers, habitat was much more favorable for the copperhead there. In southeastern Oklahoma, Trowbridge (1937:298) noted that copperheads had decreased greatly in the last decade due to killing by man, but in northeastern Kentucky, Welter and Carr (1939:130) noted that copperheads had increased over a period of years, and they attributed this fact in part at least to the creation of the Cumberland National Forest, resulting in abundant cover for the snakes. Anderson (1942: 215) wrote that copperheads were still found in Swope Park in Kansas City, Missouri. Minton (1944:474) noted that in Indiana copperheads were difficult to eradicate, even in populous areas, and that a few survived even in thickly populated hills on the outskirts of New Albany. Neill (1948:112) wrote that copperheads were found in large numbers in the northern outskirts of Augusta, Georgia, where a rock outcrop adjoining a golf course provided a favorable denning area. Conant (1952:14) wrote that the species persists across the Hudson River from New York City, in the Blue Hills near Boston, at Valley Forge near Philadelphia, and within the city limits of Washington, D. C. Oliver (1958:43) recorded that the last copperhead found inside New York City was in the Bronx in 1936, and that in 1954 a single individual was killed in the Greenbrook Sanctuary in Alpine, New Jersey, within sight of New York's skyscrapers.

Control

Techniques for controlling venomous snakes have not been satisfactorily developed. The bounty system has been most widely tested. It has been used against many kinds of snakes in various parts of the world, but in most instances no noticeable decrease in their numbers has resulted, and the financial outlay has been great in some instances. As usual with the bounty system, abuses have been common. The practices of keeping gravid females in captivity to obtain large numbers of young to submit for bounty, and of bringing in snakes found already killed by traffic on roads, or those killed in distant areas, to claim bounty from the granting agency of the state or county have often contributed to the breakdown of the system.

South Dakota has long employed a rattlesnake-control officer. Mr. A. M. Jackley held this position for many years and became an expert in the mass extermination of rattlesnakes. Jackley's chief method consisted of clubbing or trapping the snakes as they emerged in large numbers from a hibernation den. Trapping was accomplished by partly closing the exit with cement, leaving only a narrow passage leading through a trap-door into a large wooden box where the snakes accumulated as they emerged. Although the technique was especially adapted to the conditions on the northern Great Plains, it is obvious that snakes which congregate in large numbers to hibernate are thereby rendered more vulnerable to effective control operations. Mass slaughter of snakes (especially rattlesnakes) by clubbing, shooting and blasting in the vicinity of their hibernation dens has long been a common practice in various parts of the United States. However, in most instances the dens involved in these raids have been in areas remote from human habitations, where the presence of the snakes involved no special problem. Rather, motivation for the killing has been the desire for sport or an ingrained dislike of snakes, or the fancied prestige gained by the recounting of exploits, perhaps substantiated in part by a display of numerous skins and rattles.

To my knowledge the copperhead has never been subjected to systematic control operations, but in the course of my field work I received several inquiries as to how such control operations should be carried out. Details of the copperhead's natural history and ecology such as those set forth in this report provide a background essential in the planning of any control.

Because of the copperhead's abundance and widespread range, control operations against the species as a whole are impractical. Also it is by no means certain that control operations resulting in complete suppression of the species would be desirable. Besides the harmful and obvious effects of its bite, the species affects man in various ways; the sum total of the beneficial effects may more than compensate for the occasional harm. Through its food habits, especially, the copperhead affects the ecosystem where it occurs and the prey consists chiefly of animals that are generally considered to be harmful. However, in local areas, such as remaining blocks of woodland in suburban communities, where the copperhead may be a distinct hazard especially to small children, if at all common, its control is desirable, and should prove to be feasible.

An obvious method of control is by reducing the food supply. Wherever the species is abundant small rodents such as white-footed mice (*Peromyscus* sp.) and/or voles (*Microtus* sp.) or perhaps other small vertebrates such as shrews, lizards or frogs, are sure to be common, providing the chief source of food. Control of the small rodents on a limited area ordinarily would be accomplished easily by use of poisoned baits. With the chief food supply removed the snakes would be starved out eventually. However, quick results could not be expected because the copperhead's capacity for fasting would permit individuals to survive throughout their entire season of activity without any food. Even though the population of small mammals had been reduced to a low level by control operations, the high reproductive potential characteristic of most small mammals might permit building up to moderate or high numbers again soon enough to save the snakes from starvation unless the original operations were followed up at suitable intervals.

More effective control could be applied when copperheads were concentrated in their denning areas along rock ledges, in either spring or fall. Dynamiting of snake dens (usually those of rattlesnakes) has often been attempted, sometimes with spectacular results. However, where shelter suitable for hibernation is abundant, the hibernating population might be much too well dispersed to be appreciably affected by dynamiting. On the 590 acres of the Reservation, for instance, the many hundred copperheads certainly hibernate in scores of different crevices and few could be killed with any one charge of dynamite.

Klauber (1956:978) mentioned the possibility that blasting of dens (of rattlesnakes) might open up deeper or more extensive cavities favoring the survival and ultimate increase of individuals not killed in the blast.

Use of poison gas has often been tried as a means of killing snakes in their dens, but usually without much success (Uhler, 1944:8; Klauber, *op. cit.*:983). The low rate of metabolism in snakes, especially when they are dormant or partly so in their dens, renders them unusually resistant to the effects of poison gas.

Flattery (1949:16) found nicotine sulphate to be highly toxic to snakes, and succeeded in killing large numbers of garter snakes (*Thamnophis* sp.) by putting out metal trays with half an ounce of nicotine sulphate dissolved in about 2½ quarts of water where the snakes were so abundant as to be considered pests. The pans were covered with wire mesh to keep out other animals. The snakes were attracted to the water and were killed by the hundreds, but it seems doubtful whether the population in the general area was appreciably affected.

Chemical sprays would be far more effective. Commonly used insecticides such as DDT, aldrin, dieldrin, toxaphene and heptachlorane are highly toxic to all kinds of reptiles. Experiments in which tracts of woodland or marsh were sprayed from planes with sufficient concentrations to eliminate insect pests have been shown to have devastating effects on the local populations of reptiles (Mills, 1952:289). Much wildlife of harmless and beneficial species is destroyed by the indiscriminate broadcasting of such poisons, and the cost per acre is high. Against copperheads most economical and efficient control could be obtained by use of high concentrations in a hand sprayer, with repeated heavy applications in April and October along the rock ledges where the snakes concentrate, with special attention to the holes, fissures, and crevices, which might serve as dens. In summer, applications of the same concentrated spray might be effective in killing snakes along rock walls, hedges, weedy fence rows and clumps of shrubbery which are the types of places where copperheads are most likely to hide or travel in the infested areas.

Smith (1953:1) and Minton (1951:322) have emphasized the importance of removing from one's premises potential shelter for venomous snakes such as old boards, shingles, wood slabs, cardboard cartons, scraps of tarpaper, rock piles and vegetation such as weed patches, high grass, and clumps of shrubbery. Such shelter renders the habitat more attractive to the small animals that provide the copperhead's food, and to the copperhead itself. The snakes may be attracted from nearby areas by abundant cover and their chances of survival and successful reproduction may be increased.

THE VENOM AND BITE

Adaptations Correlated With the Venom

In venomous snakes the salivary secretions of the supramaxillary or parotid glands serve to subdue the prey. In the more primitive groups including many opisthoglyph and proteroglyph types, the development of toxic saliva and of teeth specialized as fangs to inject the venom has involved no evident modification in the snake's general habits or mode of life. But in the more specialized groups, notably the true vipers (Viperidae) and especially the pit vipers (Crotalidae) the development of a more advanced type of venom and injection apparatus is accompanied by other structural modifications, and by increasing commitment to a mode of life different from those of the more primitive snakes. In both groups of vipers the body tends to be short, stocky and flattened. The head is triangular and widened posteriorly to accommodate the enlarged venom glands. The maxillary bone, bearing a single functional tooth, the specialized poison fang, has become much shortened, permitting it to rotate on a horizontal transverse axis, and the rigidly attached fang folds back along the roof of the mouth when not in use. By virtue of this device the true vipers and pit vipers have been able to develop poison fangs that are relatively much longer than the teeth of any other snakes. Using these specialized teeth in biting their prey, they are able to penetrate deeply into the vital organs and inject the venom where its action is most rapid and effective. Typically, these snakes are nocturnal and feed upon relatively large prey animals, gorging themselves at each meal with long intervals of fasting. They are sluggish and hunt chiefly by lying in wait to ambush the prey rather than by active search.

The copperhead is regarded as one of the most primitive of the pit vipers, yet it is fairly typical of the group as a whole. In retaining the large cephalic shields in a pattern similar to that of typical colubrine snakes, it differs from the more specialized crotalids (*Crotalus, Bothrops, Trimeresurus*) in which the shields tend to break up into small, granular scales—a tendency correlated with widening of the head and enlargement of the venom glands. The relatively short fangs and weak venom in the copperhead also seem to reflect its primitive position in relation to the other pit vipers. In general habits it is typical of the group, being slow and sluggish in most of its movements, somewhat secretive, and nocturnal. Like the majority of vipers it is terrestrial although partly aquatic, fossorial and arboreal types have evolved among its more specialized relatives. Like the other crotalids the copperhead preys mostly on vertebrates and especially mammals, but is unique in its liking for large caterpillars and cicadas, perhaps retained from a more generalized ancestral stock that preyed on invertebrates to a greater extent.

The primary function of the venom is to cause rapid death in the small animals that are the usual prey, rather than to cause death or damage in humans or other natural enemies. From this viewpoint the copperhead's venom apparatus is as adequate and efficient as are those of other crotalids, although some of these are far more dangerous to humans. In a typical bite the fangs penetrate the thoracic or peritoneal cavity of the prey, but rarely penetrate farther than the subcutaneous layer in a human victim.

Porges (1953:50) in discussing the action of snake venom, stated: "Snakes cannot chew and mix the products of their salivary glands with the tissues of their prey. Instead they use a highly developed injection apparatus to apply digestive agents to their food." The action of enzymes plays an important part in the digestion of the prey. The saliva of poisonous snakes contains certain powerful enzymes that are not produced by other kinds of animals, notably ophio-oxinase. Porges stated that the tissues of a rat injected with venom are digested about twice as rapidly as those of an uninjected rat.

Properties of the Venom

The venom is a slightly viscous, watery liquid, yellowish but varying from almost colorless to bright yellow or orange. Often it is cloudy, especially in large individuals; it is almost clear in some young. When copperheads are handled, they usually open their mouths in the course of their struggles and in some individuals the venom can be seen, mixed with other secretions in the buccal cavity. Struggling copperheads commonly erect their fangs, moving them jerkily and opening and closing the mouth in an attempt to bite. As the jaw muscles are contracted, venom often trickles from the tips of the fangs and can be forcibly projected for two feet or more in a spray of fine droplets.

Githens (1931:82 and 1935:166) described the venom of pit vipers as a viscid yellow liquid containing from one-third to one-fourth solid matter, a complex mixture of mucous, fatty compounds, salts, epithelial debris, and several protein poisons which act upon the blood, walls of the blood vessels, the central nervous system, and other tissues.

Snake venom has many components, each with its different damaging effect on the body of the victim, who may succumb from any of a number of different causes. The cause of death may differ according to the species of the victim, the site of the bite, the quantity of venom injected, and of course, the kind of snake delivering the bite. The immediate cause of death may be paralysis of the central nervous system, or of the myoneural junctions, or of respiratory centers; it may be stoppage of the heart, or asphyxiation from massive intravenous clotting (Ghosh and Sarkar, 1956:191); or in more lingering cases it may result ultimately from the cumulative effect of more generalized tissue damage, including destruction of the erythrocytes and the walls of the blood vessels. Even if the victim survives all these effects, he may succumb eventually to bacterial infections which thrive in the damaged tissues. The mouths and fangs of snakes are septic and some bites seed the wound with infectious microörganisms.

Besides the toxic components in snake venom, there are relatively non-toxic substances which promote rapid spreading of the venom through the body of the victim. Buckley (1959:96) stated that permeation of the victim's body is accomplished largely by enzymatic activity. Jacques (1956:291) attributed the rapid spreading of the venoms of snakes and other poisonous animals to their hyaluronidase content.

Comparing symptoms in victims bitten by various crotalids, Hutchison (1929:50) noted that respiratory difficulty, an expression of the neurotoxic effect of the venom, is most pronounced in cases of poisoning by the copperhead, timber rattlesnake and western diamondback. In humans the bite of a copperhead does not cause extensive hemorrhage as do those of rattlesnakes or cottonmouths. Smith (1956:307) stated that serious secondary infections seldom occur after copperhead bites, although they almost always accompany those from rattlesnakes.

Copperhead venom has found medical uses, as a local coagulent, and in the treatment of epilepsy, neurasthenia, chorea, and shell-shock (Allen and Maier, 1941:249).

Quantity of Venom Produced

Amaral (1928:104) presented figures showing the amounts of venom secreted by copperheads, along with thirteen other species of "nearctic" pit vipers totalling several thousand specimens. Average amounts of liquid and dried venom, respectively, for copperheads of various categories were: young—.14 cc., 40 mg.; adults—.18 cc., 50 mg.; old adults—.21 cc., 60 mg.; exceptional individuals—.26 cc., 75 mg. The categories were not defined. The figures seem somewhat misleading in implying a rather narrow range of variation between individuals of different size and age categories in the yield of venom. A large adult male copperhead may be as much as thirty times the bulk of a newborn young, and their yields of venom would presumably be somewhat proportional to their weights, although in the young the head and venom glands are relatively large. Githens (1935:167, Table 1) indicated that in 80 copperheads "milked" for venom, the yield of dried venom per snake averaged 56 mg. (maximum 90). Keegan (1956:414) gave 50 mg. as the average amount of dried venom obtained at each milking from a copperhead, and he estimated that in delivering an effective bite the snake may inject from 25 to 75 per cent of the contents of its venom glands.

Toxicity of the Venom

Githens (1935:171) performed extensive experiments to determine the toxicities of various crotalid venoms. For the copperhead the average minimum lethal dose of dried venom for a 350-gram pigeon intravenously injected was found to be .12 mg. (.20 mg. to .05 mg.). Thus an average adult copperhead would have sufficient venom to kill 470 such pigeons, each having many times the bulk of the snake's normal prey. Githens emphasized the fact that in his tests of venom the factor measured was power to cause acute paralytic death in the experimental animals. In the more primitive types of venomous snakes, including the elapids and the less specialized crotalids, the neurotoxic components of the venom are relatively more prominent, while in the more specialized of the pit vipers, according to Githens, the hemolytic components of the venom are more developed. This hemolytic type of venom produces far more severe local symptoms, and more lasting effects—if the victim does not soon succumb.

Describing the difference in effect according to the amount of venom, Githens (*loc. cit.*) wrote: "When given intravenously, especially in excessive doses, the venom may kill within five to ten minutes by convulsions apparently asphyctic, and perhaps due to interruption of the circulation by intravascular clotting. After somewhat smaller doses, paralysis is the usual manifestation. This begins in pigeons usually within fifteen minutes, as a weakness of the legs, the pigeon settling to the floor of the cage. As paralysis advances, the neck becomes weak, the beak, and finally the entire head resting on the floor. After this stage is reached, recovery is rare. According to the dose, paralytic death may result in from fifteen minutes to twelve or eighteen hours." Effect of the venom is, of course, maximal when injections are intravenous.

Using pigeons intravenously injected, as the experimental animals Githens tested the potency of 26 kinds of American crotalids, mostly rattlesnakes. If copperhead venom, with average minimum lethal dose of .20 mg. is used as a standard of comparison, with a rating of one unit, other kinds had the following relative potency (numbers in parentheses represent number of assays): red rattlesnake (*Crotalus ruber*) .2 (5), black-tailed rattlesnake (*C. molossus*) .4 (6), Florida diamondback (*C. adamanteus*) .4 (8), timber rattlesnake (*C. horridus*) .6 (12), western diamondback (*C. atrox*) .9 (29), sidewinder (*C. cerastes*) 1.0 (4), cottonmouth (*Agkistrodon piscivorus*) 1.1 (16), cantil (*A. bilineatus*) 1.1 (2), Great Basin rattlesnake (*C. viridis lutosus*) 1.1 (11), South American rattlesnake (*C. durissus*) 1.1 (22), Pacific rattlesnake (*C. viridis oreganus*) 1.2 (11), massasauga (*Sistrurus catenatus*) 5.0 (6).

Minton (1953:214) studied variation in venom samples from seven timber rattlesnakes and eight copperheads. He found that in the copperhead samples the strongest was three times as toxic as the weakest. Even greater variation in toxicity occurred in the seven samples from the timber rattlesnakes. Expressed in terms of the intraperitoneal "lethal dose 50" (the dose capable of killing half the experimental mice receiving injections of it) Minton found that of the rattlesnake venom 5.11 milligrams per kilo was required and of the copperhead venom, 6.36 milligrams per kilo. Thus the rattlesnake venom averaged approximately 1¼ times as potent as the copperhead venom. In discussing the validity of his findings with regard to probable effect of the venoms on humans, Minton pointed out that the mouse is relatively more resistant to the venom than is a human, and that intraperitoneal injection is not normal in snakebite when a human is the victim. However, he stated ". . . there is every reason to believe that the bite of a snake whose venom contains approximately ten thousand mouse lethal doses per milliliter would be considerably more serious to a human than the bite of a snake whose bite contains only about two thousand doses in the same volume. This limited study indicates that wide and apparently unpredictable individual variation in venom toxicity occurs among copperheads and timber rattlesnakes and probably among other species as well."

However, in later publications, Minton (1954:1079 and 1956:146) arrived at much different figures for the toxicity of these venoms on the basis of subcutaneous injections in mice. The "lethal dose 50" per kilo of body weight of the victim of the copperhead was found to be 25.65 mg. Approximately the same potency was determined for the cottonmouth. Other crotalids tested were all more potent than the copperhead, in the following ratios (considering the copperhead's potency to be one unit): pigmy rattlesnake (*Sistrurus miliarius*), 1.06; red rattlesnake, 1.23; western diamondback, 1.33; cantil, 1.35; Florida diamondback, 1.76; timber rattlesnake, 2.8; sidewinder, 4.7; massasauga, 4.9; southern Pacific rattlesnake, 7.2. Minton did not indicate the sizes of the samples on which these later figures were based, nor did he comment on the seeming discrepancies between these and his earlier figures.

Criley (1956:378) used intravenous injections of venom on 18-gram mice to determine LD 50. Projecting his figures to the same units that Minton used, the LD 50 per kilo of body weight of victim was 6.95 mg. in the copperhead. The relative toxicities of other crotalids tested, considering the copperhead to be one unit, were: Mexican West Coast rattlesnake (*Crotalus basiliscus*), .6; cottonmouth, 2.0; Pacific rattlesnake, 2.7; cantil, 4.3; Florida diamondback, 4.5; prairie rattlesnake, 6.3; South American rattlesnake, 55.0.

Minton (1956:146) also compared the hemaglutinin, local necrotizing action, hemolysin, and *Paramecium* lysin in several crotalid venoms. The three species of *Agkistrodon* were found by Minton to have similar venoms, of a type representing relatively primitive crotalid stock, with low lethal toxicity, relatively little necrotizing action, and well developed hemaglutinin and hemolysin. Minton noted that among the eleven species tested relationship between the intraperitoneal and subcutaneous lethal dose showed considerable variation. "The greatest difference was observed with the venom of *S. catenatus* where the intraperitoneal LD 50 is approximately one-twentieth the subcutaneous LD 50. By way of contrast, the intraperitoneal LD 50 for *C. horridus* venom is approximately two-thirds the subcutaneous LD 50." Obviously the copperhead made a relatively better showing when its partly neurotoxic venom was injected intraperitoneally or intravenously than when it was injected subcutaneously, and made a far better showing on the pigeon than it did on the mouse.

There has been some difference of opinion concerning the capability of young copperheads in producing venom and in delivering an effective bite. Reese (1926:357) related an instance of three newborn copperheads in captivity which repeatedly bit a rat placed in their cage without harming it. To test further the lack of potency in these young snakes Reese sacrificed them, ground up their venom glands, and injected an extract of the glands into young rats. The rats were not killed, but both earlier (Atkinson, 1901:152) and later tests have failed to substantiate the idea that newborn young of copperheads and other pit vipers lack effective venom.

Stadelman (1928:67) caused a newborn copperhead to bite his forearm for 60 seconds. Symptoms were relatively severe. Swelling steadily increased for 21 hours and subsequently did not lessen for the next twelve hours, subsiding gradually from the second to the seventh day after the bite. In further experimentation on the same subject, Stadelman (1929:81) resorted to use of a mouse as the experimental animal. He removed a captive-born copperhead from its fetal membranes and forced it to bite the leg of the mouse. The animal died in 48 hours. Stadelman observed that the biting mechanism is not well co-ordinated in the first few hours after birth.

Susceptibility of Snakes

There has been much controversy and misunderstanding regarding the susceptibility of venomous snakes to their own poison. In the course of my study many copperheads that were disturbed were observed to bite themselves or other individuals, and the results varied, from no perceptible effect at one extreme, to almost instantaneous collapse, and death within a few minutes (Fitch, 1959: 21) at the other. If venom from a bite is injected into a vital organ, death may soon ensue, but ordinarily the recipient of the bite shows but little ill effect. A copperhead that is being handled will sometimes bite through its own lower jaw by suddenly closing its mouth while the fangs are erect. Such bites sometimes cause severe temporary swelling of the chin and inflammation of the lining of the mouth. When a copperhead that is forcibly restrained bites its own body as a coil comes within reach in the course of its writhing, the damage is usually slight.

Ring-necked snakes were often offered alive to young copperheads in captivity, and when bitten they usually died within a few minutes—as rapidly as any mammals. Keegan and Andrews (1942: 253) experimentally tested the venom of copperheads and rattlesnakes on many kinds of snakes, and found that all were susceptible, the ring-necked snake particularly so. Only one of 21 snakes tested by Keegan and Andrews with more than .233 mg. of venom per gram of body weight survived. However, it is noteworthy that this is more than 650 times the lethal dose (injected intravenously) for a pigeon of comparable size.

Allyn (1937:222) experimented with a copperhead, a timber rattlesnake and a massasauga, causing each snake to be bitten at mid-body by the other two. In each instance there was slight swelling and the bitten snake was more sluggish than usual for several days, but recovered eventually. Swanson (1946:242-249) also experimented to determine and compare the effects of the venoms of North American crotalids on various snakes, including both harmless and venomous species. He found that snakes usually are able to survive normal or average doses of venom, although they are by no means immune to it. Copperheads curiously, proved to be more susceptible to venom of their own species than to other snake venom. Four minims killed a copperhead in 15 minutes; 2 minims in a half hour; 2 minims in 20 minutes; 1.5 minims in 5 hours; all snakes were of comparable sizes. Ten injections of copperhead venom (2.5 minims to 10 minims) into other kinds of snakes (water moccasin, massasauga, timber rattlesnake, common water snake, yellow-bellied racer, black rat snake, milk snake) all resulted in death in from 35 minutes to 29 hours and 45 minutes.

PLATE 13

FIG. 1. Marking of a copperhead; the snake is held immobilized, its neck and tail firmly grasped in the left hand while the subcaudal scales are clipped with sharp scissors. × 1/5.

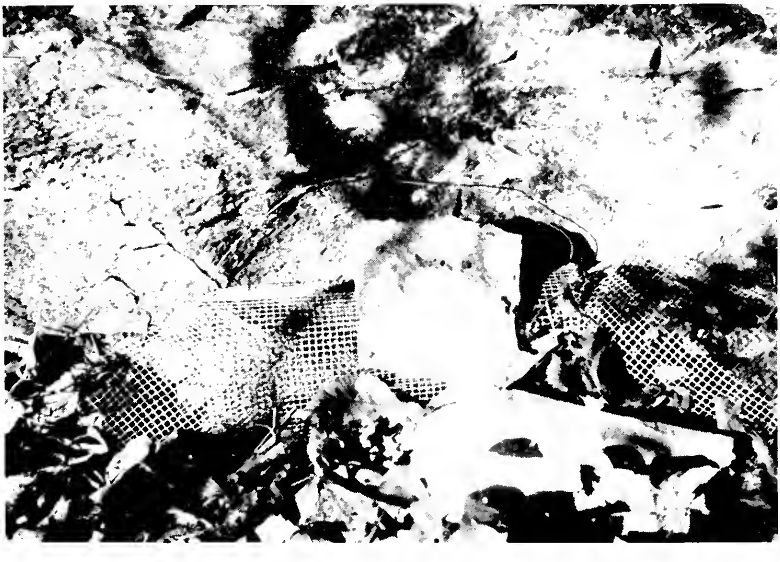

FIG. 2. Wire funnel trap set for copperheads at base of rock face of southward exposure, October, 1959. × 1/6.

PLATE 14

FIG. 1. Brushy field with dense herbaceous vegetation, a favorable habitat for copperheads in summer, 100 yards east northeast of Reservation headquarters, July, 1959.

FIG. 2. Prominent hilltop limestone ledge with deep fissures, "Rattler Ledge" on the Rockefeller Experimental Tract, April, 1959. Numerous copperheads along with timber rattlesnakes and various harmless snakes hibernated in this vicinity.

Fig. 1. South-facing rock ledge at site of old quarry in May, 1959. The rocky and brushy habitat with woodland and grassland rendered this a favorite location for copperheads throughout the season of their activity.

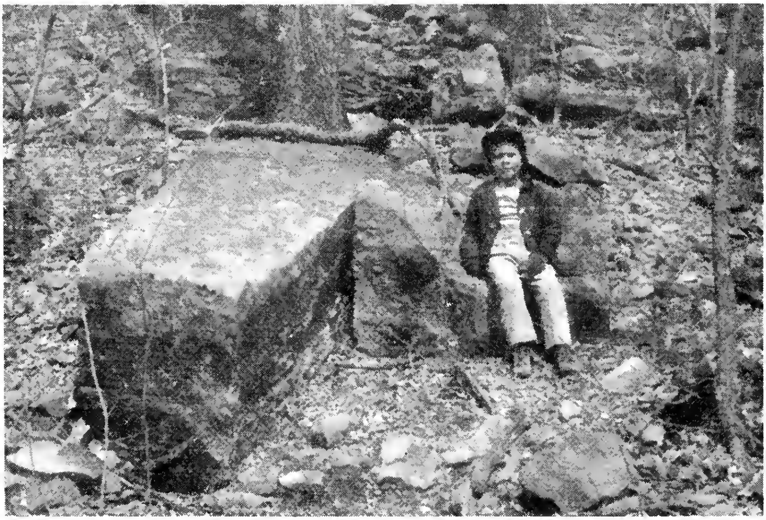

Fig. 2. Massive limestone slab at lower ledge on a southwestern exposure. Each autumn copperheads were trapped at the base of this slab. The cleft to the boy's right was believed to be the entrance to a hibernation den, November, 1958.

PLATE 16

FIG. 1. Trans-Pecos copperhead (approximately × ¼) in live-oak grove at Independence Creek, Terrell County, Texas. Sheep grazed in this vicinity and herbaceous vegetation was scanty; June 28, 1957.

FIG. 2. Remnants of live-oak grove devastated by flood, with piles of drift and debris, at Independence Creek, Terrell County, Texas, June 28, 1957. The flood in June, 1954, destroyed much of the oak-grove habitat and drastically reduced the population of copperheads locally.

PLATE 17

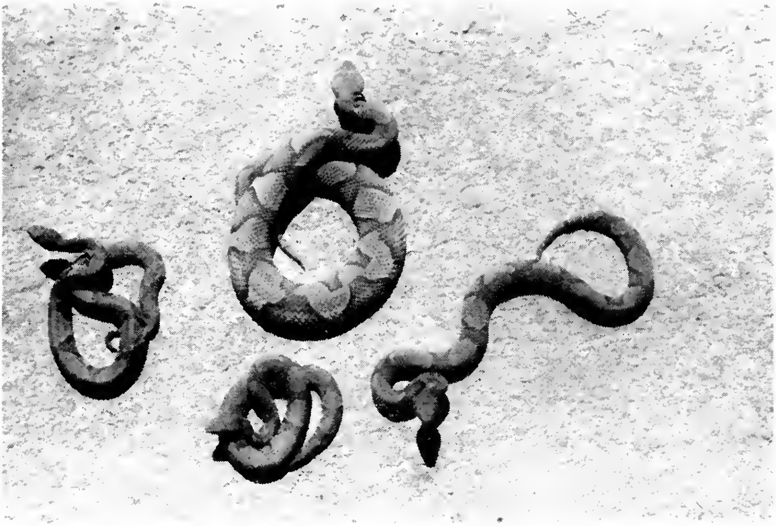

FIG. 1. Two-year-old female copperhead (above) reared in captivity; three recaptured marked young (below) of the same age but smaller bulk; approximately × $^{2}/_{7}$, May, 1957.

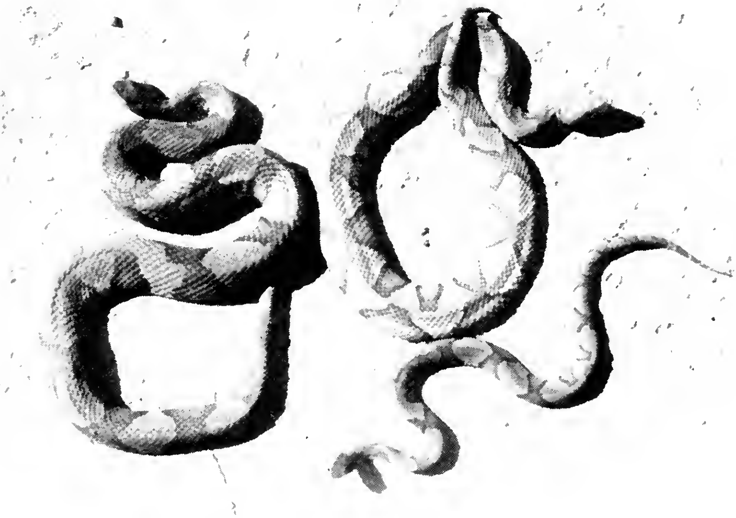

FIG. 2. Large adult male (left), large adult female (right) and newly matured two-year-old male showing differences in length and bulk; approximately × $^{2}/_{7}$, October, 1958.

Fig. 1. Head of live male 41-inch copperhead, × 2, showing physiognomy, scalation, and pattern; July 5, 1960.

Fig. 2. Large adult male and one-year-old male, approximately × ⅔ showing difference in size, September 13, 1951.

FIG. 1. One-year-old copperhead (left), two-year-old (middle) and new-born young showing differences in size. (Approximately $\times \frac{2}{5}$.)

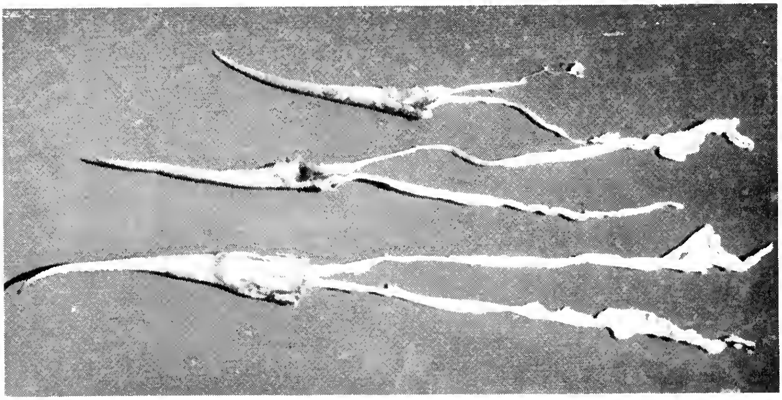

FIG. 2. Tails and reproductive organs of female copperheads: upper, three-year-old still not sexually mature; middle, adult that had not borne young recently (left ovary missing); lower, adult, recently parturient, with enlarged oviducts, October, 1959. (Approximately $\times \frac{1}{3}$.)

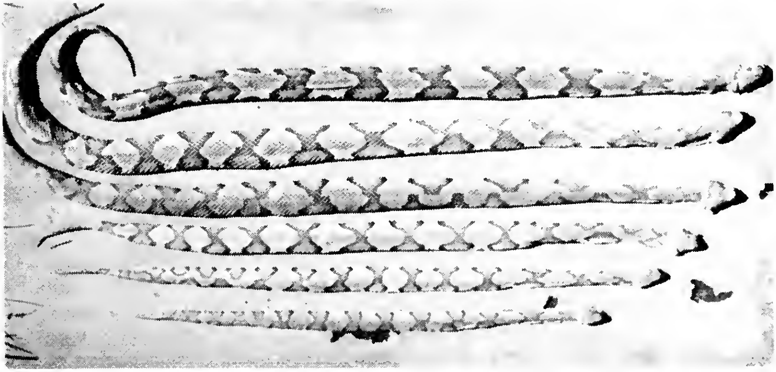

FIG. 3. A group of copperheads from Buck Creek, seven miles southwest of Clinton, Douglas County, Kansas, showing irregularities in the dorsal cross-bands, that are typical of the population studied, April, 1959. (Approximately $\times \frac{1}{5}$.)

PLATE 20

FIG. 1. Birth of copperheads; to the right of the female's tail a young just extruded lies enclosed in its fetal membranes. Two litter mates which preceded it lie farther to the right, likewise still partly enclosed in membranes, September, 1959. (Approximately × 2/7.)

FIG. 2. First-year copperhead (left) kept from time of birth in captivity and well-fed even when it would have been hibernating under natural conditions, and recaptured litter mate of much smaller bulk, demonstrating effect of food upon growth. (Approximately × 2/5.)

Circumstances and Outcome of Bites

In an early study of the snake-bite problem in the United States Willson (1908:516) assembled data on 740 bites of venomous snakes reported before 1908. Ninety-seven (17 per cent) of the bites were those of copperheads and five of these copperhead bites resulted in death. Willson implied that in each instance death might have been averted by better care, and that in the three adult men who died, the large amount of whiskey taken may have been the deciding factor. He expressed doubt that copperhead bite is ever fatal to adults in uncomplicated cases.

Hutchison (1929:47; 1930:40) listed the seasonal distribution of copperhead bites, for which reports had been received by the Antivenin Institute of America for the years 1928 and 1929. For 1928 the distribution was: January, February and March, 1; April, 1; May, 8; June, 21; July, 50; August, 39; September, 36; October, 6; November, 5; December, none. For 1929: January, 1; February, none; March, 2; April, 10; May, 19; June, 22; July, 37; August, 28; September, 16; October, 2; November and December, none. None of the 303 copperhead bites recorded in these two years resulted in death, although there were many deaths from rattlesnake bite. For the 200 bites of poisonous snakes (mostly copperheads) reported in Virginia from 1941 through 1953 (Wood, 1954:938) the seasonal distribution was: April, 1.6 per cent; May, 9.5 per cent; June, 16.3 per cent; July, 31.6 per cent; August, 18.9 per cent; September, 19.5 per cent; October, 2.6 per cent.

Minton (1951:320-321) tabulated the circumstances and results of copperhead bites in Indiana. The outcomes of nine bites were as follows: "Moderately severe symptoms. Recovery."; "Died. Said to have drunk a large quantity of whiskey." (The snake that inflicted this bite, in Crawford County, Indiana, had been called a moccasin, but no cottonmouths are known from this area and Minton suspected a copperhead or rattlesnake was the real culprit.) "Recovery." "Uneventful recovery." "Severe serum reaction; recovery." "Recovery." "Recovery after rather prolonged illness." "Moderate symptoms with good recovery." In four instances the bite was on a finger, in three it was on a hand, and twice on a foot. Circumstances of the bites were summarized as follows: "Playing near a woodpile." "Working on construction gang near river." "Touched snake while climbing among rocks." "Measuring captive snake." "Picked up snake—mistaken for harmless species." "Transferring captive snake from cage to bag." "Moving a large rock in woods." "Reached into empty feed sack." "Playing in abandoned woodshed." "Reached into corn crib." Swartzwelder (1950:578) recorded copperhead bites in Louisiana while: "Trapping in marshes" (two instances); "playing around lumber," "stepping on snake," "in outbuilding," "picking moss," "hunting." Wood (1954:942) recorded the circumstances of a less typical accident in Virginia, as follows: "A camping party near Luray decided to sleep in a barn, and shortly after retiring one of the campers complained of a wasp sting on her right arm. About two hours later another member of the party was awakened by a stinging sensation on her thigh. A flashlight revealed the presence of a copperhead nearby, and examination of the wounds showed the deep twin punctures made by fangs of such a snake. . . . It is probable that the copperhead was foraging, detected the presence of a warm object with its 'heat-receptor' pits, and struck, injecting sufficient venom to immobilize its usual prey."

It is significant that three of the ten cases recorded by Minton involved handling of live copperheads. It is my impression that a similar ratio obtains in Kansas. Many of the copperhead bites that have come to my attention were sustained by persons handling the snakes, often motivated by curiosity or bravado.

Githens (1935:165) in his tabulation of 2,342 snake-bites sustained in the period 1927 to 1934, indicated that 163 of the bites were received by persons who were intentionally handling poisonous snakes. Of the 72 persons who died from effects of bites of venomous snakes more than half were children less than 14 years old. Of the 2,342 total, from all parts of the country, 691 were those of copperheads, far more than were inflicted by any other species. The timber rattlesnake, with 411 bites, was second. Among 134 snake-bite cases in Virginia for which the species were known, the distribution was: copperhead, 119; timber rattlesnake, 12; canebrake rattlesnake, 2; cottonmouth, 1 (Wood, 1954:937). In Louisiana the cottonmouth is the chief offender and the copperhead figured in only 11 of 161 bites (Swartzwelder, 1950:579). Swaroop and Grab (1956:441) estimated that there are from ten to 20 deaths annually in the United States from snake-bite, and they mentioned the diamondback [both species?], prairie rattlesnake and cottonmouth as the chief killers. Certainly the copperhead is relatively unimportant as a cause of death, despite its prominence in snake-bite statistics.

Hypersensitivity to Venom

Zozoya and Stadelman (1929:94) described an instance of hypersensitiveness to snake venom in a 22-year-old man who was employed in the handling and collection of the venom. He had been bitten by a copperhead in June, 1923, and in later years received injections of the venoms of *Crotalus, Agkistrodon, Bothrops* and *Naja*. In August, 1928, he was again bitten by a copperhead. Late in 1928 the hypersensitiveness became evident, and increased in intensity over a period of weeks, with coryza and violent sneezing resulting whenever the dried venom was handled. Mendes (1952:

1328) described the case history of a 29-year-old woman who, after working at the Antivenin Institute at São Paulo, Brazil, for two years, developed acute asthma, rhinitis, and conjunctivitis upon proximity to the venom. These symptoms continued for eight years until the subject transferred to other employment; then they promptly disappeared. Cutaneous tests had shown strong reactions to venoms of *Bothrops* and *Crotalus.* No bites or injections of venom were mentioned in this account. Such hypersensitivity seems to be common in persons who handle snake venom habitually. Stanic (1956:181) stated that several members of the staff at the Central Institute of Hygiene, Zagreb, Yugoslavia, became hypersensitive in varying degrees to venom of vipers, and he described a desensitizing procedure which was partially successful for several months, but the hypersensitivity gradually returned. Parrish and Pollard (1959) studied the effects, on man, of repeated bites by poisonous snakes. Of 13 patients tested, four gave evidence of hypersensitivity to the venom, manifested by large wheals with pseudopods. None of the patients had experienced anaphylactic shock as a result of a second bite. However, the authors stated (*op. cit.*:284): "It seems entirely possible that occasional deaths from snakebites, in individuals who have been previously bitten, may result from snake venom allergy." The authors found that a bite by one kind of venomous snake might confer sensitivity to a closely related kind.

Case History of a Bite

A copperhead bite that I received in 1957 was perhaps fairly typical, and unusual opportunity to observe the effect of the venom was afforded because treatment was kept to a minimum, emotional shock occasioned by a horror of snakes was not involved, and symptoms were set down in writing as they occurred.

The bite was received at 8:15 p. m. on June 5. Driving on a county road near the Reservation, shortly after dark in a light rain, I saw the copperhead crossing in front of the car in the glare of the headlights, swerved to miss it, and stopped the automobile a few yards beyond. I ran back with a flashlight and located the snake, a large one, which was thrashing and lunging in an energetic attempt to gain the shelter of dense vegetation by the roadside. As I confronted the snake attempting to pin it with a foot ruler, an approaching automobile rounded a curve 200 yards away, and the glare of its headlights dazzled me. The snake did not deviate from its course, but sparred with me and lunged sideways partly avoiding the stroke as I pinned down its forebody. As a result, it was held down too far back behind the head and an instant later outreaching me, it struck the middle finger of my right hand. Besides the slight lacerations made by the pterygoid teeth there were two distinct fang punctures 1⅛ inches apart, one on the dorsal surface of the proximal knuckle joint, the other on the fleshy medial surface of the finger at approximately the middle of the basal segment. Immediately abandoning the snake, I concentrated on treatment of the bite, sucking hard and drawing small amounts of blood from the fang punctures. Spasmodic twitching of muscles at the site of the bite was soon noticeable. From the start there was a dull ache at the site of the bite. Over several hours it became progressively more severe.

No tourniquet was applied on the theory the bite certainly would not be fatal and that the venom could best be dealt with by absorbing it rather than allowing its effects to concentrate at the site. No physician was consulted.

By 8:25 p. m. the site of the bite had become noticeably swollen and discolored. As a result of the swelling blood could no longer be sucked from the wound, and throbbing pain had become severe. At 8:30 p. m. to promote bleeding, three punctures were made with a 26-gauge hypodermic needle, and two aspirin were taken to alleviate pain. Bleeding from the needle punctures rapidly diminished as the swelling increased. By this time it was becoming evident that relatively little venom had been injected through the fang puncture on the knuckle joint. Probably the fang tip had struck bone near the surface preventing complete penetration of the slit end with the result that venom ejected had been partly spilled. Swelling was steadily progressing proximally. Site of the most severe pain had shifted from the lower fang puncture to an area about one inch in diameter in the palm adjacent to the base of the middle finger. The throbbing was accompanied by a sensation of numbness in the overlying skin. With a sterile razor blade a longitudinal incision half an inch in length was made through the fang puncture to a depth of approximately ⅛ inch. For several minutes thereafter blood flowed freely from the wound, but gradually it again became more meager as swelling increased, and soon little could be obtained by sucking. No further incisions were made. At 10:00 p. m. pulse was 58 (normal) and temperature was 99.0°. Swelling had progressed to a level about 2½ inches above the wrist, with slight accompanying discoloration. By 10:15 p. m. swelling had progressed to a level about four inches above the wrist. The throbbing pain in the palm was still severe and extended back along the lower side of the arm to the elbow. One-fourth grain of codeine and a glass of milk were taken. At 10:30 p. m. respiratory congestion had become noticeable. An antihistamine (Chlorotrymatron) was taken to counteract these symptoms; pulse 50. At 10:45 p. m. pain had reached its maximum, and was intense in the palm near the base of the middle finger, extending back as far as the elbow. Another ¼-grain of codeine was then taken. At 11:15 p. m. a feeling of nausea became prominent. At 11:30 vomiting occurred; pulse 55. At 12:45 a. m. no new symptoms had appeared; a sleeping capsule, nembutal grains 1½, was taken. At 2 a. m. another 1½ grains of nembutal and ½ grain of codeine were taken. On the following morning systemic symptoms had largely disappeared. The bitten hand had swollen to nearly twice normal size and swelling extended slightly above the elbow. Swelling and soreness in the afflicted hand and elbow subsided slowly, and it was nearly a month before normal use of the hand was regained.

Treatment of the Bite

Thomas Say (1819:259) a pioneer American naturalist related from first-hand observation an instance of copperhead bite and a treatment that reflected belief in an old folk remedy. The bite was followed by rapid swelling and pain. The breast of a fowl was plucked and applied to the wound. ". . . in a few minutes the fowl died without having experienced any apparent violence from the hand of the applicant, the breast exhibiting a livid appearance." A second fowl was then laid open and placed upon the wound. The patient recovered. The "fowl treatment" is still widely believed in and sometimes practiced by rural people in various parts of the country, although it has no scientific basis. Other home remedies widely used in the past, but of no value in combating the action of the venom, and sometimes causing complications that prevent or delay recovery, are imbibing of liquor, and application of kerosene, or of potassium permanganate either powdered or in solution, to the wound.

The controversial cryotherapy for snake-bite was first used by Crum (1906:1433) in Maryland on victims of copperhead bite. Technique consisted of spraying with ethyl chloride to freeze the tissues locally, supposedly slowing the action and spread of the venom. More recently cryotherapy has been championed by

Stahnke (1953:35) but violently attacked by Shannon (1956:410) who maintains that freezing of the tissues or even prolonged exposure to water as warm as 55° F. produces serious and permanent damage and usually results in gangrene.

Regardless of other measures taken, use of a tourniquet to delay spread of the venom, and incision and suction at the site of the bite to remove it have long been standard procedures. But recent experiments by Leopold, Huber and Kathan (1957:414) with rabbits have shown that both use of a tourniquet, and incision and suction shorten the time to death in the experimental animals. Rabbits that were immobilized and injected with venom survived nearly four times as long as the controls, which were given the same amount of venom but were permitted to move about freely. Parrish (1956:403) recommended early and extensive excision of tissue at the site of the bite combined with suction in serious cases after he had performed experiments in which two-thirds of the dogs injected with six MLD each were saved by such treatment, while others similarly injected, and treated with the customary incision and suction, all died.

Antigenic serum effective against the venom of "Nearctic Crotalidae," including the copperhead, was first manufactured in the late nineteen-twenties by the Antivenin Institute of America. Over periods of months horses were immunized by small but gradually increasing dosages of the venoms of eleven kinds of American crotalids. Although the serum has unquestionably saved many lives, its performance proved to be somewhat less effective than had been generally anticipated when it was first made available. Githens (1935:172, table 3) presented statistics showing the incidence of mortality from bites of different kinds of North American crotalids, treated with antivenin and untreated. Of 152 bites for which no antivenin was administered, five resulted in death, but there were only two deaths from 539 bites treated with the serum. For severe bites massive dosages of many 10 cc. ampules were recommended. As most persons are more or less sensitive to horse serum, such large doses usually caused untoward reactions that were often of alarming severity. In 1954 a new and much improved serum was made available (Criley, 1956:375) much more potent than the original product, yet more easily and cheaply produced. For this newer serum venoms of only four species (not including the copperhead) are used, yet it has been found to be effective against all crotalids. This serum is now manufactured and distributed exclusively by Wyeth Laboratories, Inc.

In the eastern states and especially the Northeast, the copperhead is of increasing relative importance as the rattlesnake's numbers dwindle in the face of advancing urbanization. Antivenin serum is sold in many areas where the copperhead is the only venomous snake present, and perhaps this species figures more prominently than any other in the actual use of the serum or in its purchase and anticipated use. Since even the newer improved serum often has disagreeable and potentially dangerous effects, and since even untreated copperhead bites rarely result in death, the use of antivenin in treatment has been seriously questioned. Oliver and Goss (1952:270) stated: "Marked reaction to the horse serum may literally make the 'cure worse than the bite' and terminate in sudden death, or produce less acute signs of distress." Wood (1954:940) discussing the circumstances and treatment of snake-bites (mostly of copperhead) in Virginia, stated that no fatalities were recorded in 168 cases. But in the 90 per cent of the victims that received serum, urticaria, pruritis, and angioneurotic edema were more pronounced than in those not so treated. Klauber (1956:920) stated that the bite of a copperhead is rarely serious enough to justify the use of antivenin. Shannon (1956:407-408) wrote that antivenin is "not an unmitigated blessing. . . . Preliminary skin testing may not reveal the presence of horse agglutinins, and serious delayed reactions or even anaphylaxis may follow the use of large or small amounts." Shannon cited two instances of rattlesnake bite, seemingly not especially serious in themselves, which, when treated with antivenin resulted in violent and prolonged anaphylactic shock. One patient was comatose for a week, the other for six days. No information is available regarding the extent to which present methods of refinement of the serum have eliminated untoward reactions.

Minton (1954:1078) found that the serum, injected into mice that had had double the minimum lethal dose of copperhead venom, conferred no perceptible protection, as all the experimental animals died. The serum was found to be in varying degrees more effective in conferring some protection on mice that had been injected with the venoms of various species of rattlesnakes. In connection with the failure of the serum against *Agkistrodon* venom, Minton commented on the fact that this kind of venom was not used in the immunization process to which the horses producing the venom were subjected. However, the antivenin used in his experiments seems to have been the older type, made with eleven venoms including that of the copperhead, not the newer four-venom preparation.

Criley (1956:374-376) explained that while the venoms of nine kinds of rattlesnakes, plus that of the cottonmouth (fifteen per cent) and copperhead (five per cent) were used in the manufacture of the original antivenin made for use against venoms of North American crotalids, the improved serum more recently manufactured is based on only four species, the western diamondback, eastern diamondback, South American rattlesnake, and fer-de-lance. Because there is strong antigenic relationship between the venoms of different crotalid genera, the use of venom from a large number of species in manufacturing serum is deemed unnecessary and undesirable. Tests have shown that antivenin made from the four species named affords the broadest possible polyvalency, and is effective against not only North American crotalids but those of the Neotropical and Oriental regions as well. Mrs. Eleanor E. Buckley of Wyeth Laboratories stated (*in litt.*, January 12, 1960): "It is the opinion of many physicians that the possible discomforts and risks in serum treatment do not equal those attendant on mechanical treatment, and recovery is certainly more rapid."

Criley (*loc. cit.*) presented figures showing that the new antivenin prepared with the four-venom formula is more effective than the older preparation against all species of crotalids (17 kinds tested, including the copperhead). Mice weighing 18 grams were given the serum intravenously. The new type serum neutralized 22.4 lethal doses of copperhead venom per milliliter in these tests. Effectiveness of the antivenin is inversely proportional to the potency of the kind of venom counteracted. In the more virulent species, *Crotalus durissus terrificus* (440 lethal doses per mg. of venom), *Bothrops atrox* (54 lethal doses per mg.), *B. neuwiedi* (44 lethal doses per mg.) and *B. jararaca* (44 lethal doses per mg.), the serum neutralized 187.0, 124.8, 90.2, and 74.8 lethal doses per milliliter, respectively. But in those kinds with weakest venom, *B. jararacussu* (3.2 lethal doses per mg.), *C. basiliscus* (5 lethal doses per mg.), and *Agkistrodon contortrix* (8 lethal doses per mg.) the number of lethal doses neutralized per milliliter of serum is relatively small—7.2, 11.5, and 22.4, respectively. Similar trends were shown in figures published by Gingrich and Hohenadel (1956:382) based in part on the same lots of venom.

The many conflicting statements in the literature, regarding the relative virulence of the copperhead's venom, and the effectiveness of serum or other remedies in combating its effects certainly emphasize the need for further investigation. However, it is obvious from the foregoing discussion that the copperhead has much less potent venom than most other New World crotalids, that the venom varies greatly in both quantity and potency between different individuals of the same population, and perhaps in the same individual at different times, and that different kinds of animals differ greatly in their susceptibility to the venom. Measures of potency may therefore show quite different results, depending on the type of damage inflicted, whether paralysis of the central nervous system, respiratory failure or massive histolysis, and on the species of experimental animal utilized.

SUMMARY

A field study of a local population of the copperhead was carried on from 1948 through 1959 on the 590-acre University of Kansas Natural History Reservation and the adjacent 160-acre Rockefeller Tract; 1,532 individuals were recorded a total of 2,018 times. Although the incidence of recaptures was low, even in the later stages of the study, the marked snakes recaptured yielded most significant data. Clipping of ventrals and subcaudals in different combinations provided formulas by which marked individuals could be recognized and the remarkably variable arrangements of the bands on the body provided a supplementary means of identification. Most of the copperheads recorded were caught in wire funnel traps. Rock ledges at hilltops where the snakes hibernated provided the most productive sites for traps. In the summers of 1957, 1958 and 1959, many funnel traps were placed in other habitats and supplemented with drift fences. In these seasons copperheads were caught in substantial numbers on their summer ranges. Records obtained on the Reservation were supplemented by records contributed by many co-operators, and by those available in published literature.

The copperhead is a medium-small snake; those from the Reservation averaged 22.4 inches snout-vent length (9.8 to 42.0 inches in over-all length). The coloration is reddish brown with seven to 16 chestnut cross-bands constricted middorsally to an hourglass shape. Maximum size is greater by one-fourth in males than in females. Most typical snout to vent lengths of adults on the Reservation are 28.5 inches for males and 26 inches for females. In the males the tails are, on the average, slightly longer than in females of the same size, but in both sexes relative tail length progressively decreases as larger size is attained.

The poison fang, a relatively elongate hollow tooth that is borne on each maxillary bone, is only about half the relative length of a typical rattlesnake fang. The fangs are shed and replaced fre-

quently. Observations on a captive copperhead indicated that typically a fang is functional for a period of approximately a month, but the interval is variable.

Nearest living relatives of the copperhead are the partly aquatic cottonmouth of the southeastern states and the cantil of tropical Mexico. The genus also includes at least eight Asiatic species, most of which, like the copperhead, are forest dwellers. This zoogeographic evidence indicates that the genus formerly was more northern in distribution and dates back to the early Tertiary, but the earliest known fossils of the genus and family are remains of the copperhead (found associated with those of the prairie rattlesnake) at Driftwood Creek in southwestern Nebraska in deposits that are probably of lower Pliocene age. The geographic distribution of the copperhead corresponds closely with the extent of the Deciduous Forest Biome of Eastern North America, exclusive of its glaciated northern part. Small isolated populations exist far to the west of the Biome's present limits where relicts of deciduous forests remain in unusually mesic situations. The subspecies *pictigaster* of Trans-Pecos Texas consists of such relict populations. The other three subspecies correspond to major subdivisions of the Deciduous Forest Biome that are based upon the dominant genera of trees prevailing. *A. c. laticinctus* is confined to the Oak-Hickory Association which is the westernmost phase of the Biome. *A. c. mokeson* occurs mainly in the combined Oak-Chestnut, Mixed Mesophytic, and Western Mesophytic subdivisions, but a disjunct western segment occurs in the Oak-Hickory. *A. c. contortrix* occurs chiefly in the Southeastern Evergreen and Oak-Pine associations. *A. c. pictigaster* differs from the others most, as it has one scale row much shortened, and seemingly the snake itself is dwarfed. The other three subspecies differ from each other mainly in pattern. *A. c. contortrix* has the "hourglass" markings and shading, which are characteristic of the copperhead, most highly developed. The copperhead lives chiefly in or near deciduous forest. Throughout most of its range it prefers rock ledges in hilly situations. In the southern states swamps and other lowland situations are frequented more than they are in other parts of the range. Where the copperhead occurs in arid regions at the western extreme of its range, the species inhabits the most mesic situations available.

The copperhead spends most of its time in a characteristic flat resting coil, with the tail on the outside and the head, neck and forebody in an S-shaped loop near the center. In this position the snake awaits approach of prey. Activity is chiefly nocturnal. In normal locomotion the snake crawls slowly, with frequent long pauses. Ordinarily a combination of the "horizontal undulatory" and "rectilinear" methods of crawling are employed. An individual moves about slowly under most conditions; in a 24-hour period it may shift only a few yards or may not move at all. There is a pronounced tendency to keep within a definite area, or home range. The areas of typical home ranges in summer were calculated to be approximately 24.5 acres for males and 8.5 acres for females but records were inadequate to map any one range in detail. A home range may include a rock ledge situation where the snake hibernates, but more often is disjunct from the area of hibernation, and the snake's movements include annual migrations from hibernation den to home range in spring and back again in autumn. Most frequently the snake returns to the same den each year. The average shift was found to be 1,715 feet for 21 males and 1,396 feet for ten females. Occasional shifts occur in hibernation dens and/or summer ranges.

Skin shedding occurs at intervals that are variable for any individual. Most typically there are probably two sheddings, or at most, three, in a growing season of approximately six months in adults.

There is much difference between individuals in their times of retirement into hibernation in autumn and emergence in spring, but on the Reservation the entire population ordinarily is dormant from the second week of November through mid-April. Hibernacula are in deep crevices in limestone outcrops along hilltops, where the exposure is to the south, east or west. Often several individuals congregate in the same hibernaculum. In autumn, even after the advent of freezing temperatures at night, the snakes may continue to emerge to bask in afternoon sunshine. At times copperheads share their hibernacula with other species of snakes, including timber rattlesnakes, racers, rat snakes, water snakes, garter snakes, and king snakes.

Copperheads are able to survive temperatures slightly below freezing but cannot survive having their body fluids completely congealed. Emergence from hibernation may occur at body temperatures in the neighborhood of 10° or 11° Centigrade. At temperatures only a few degrees lower, the snakes seem incapable of spontaneous movement and respond only to vigorous stimulation. At temperatures near freezing the snakes are completely dormant, appearing to be inert and lifeless. Temperatures between 26° and

28° Centigrade (approximately 80° Fahrenheit) seem to be optimum. Activity is largely nocturnal and basking does not occur regularly in summer except in gravid females.

Males become sexually mature in their second summer, usually many weeks before they have attained an age of two years. At sexual maturity they may be as small as 420 millimeters in snout-vent length—only half the length of a large adult and approximately one-tenth his bulk. Most females become sexually mature after their third hibernation and produce first litters when they are approximately three years old, at a minimum snout-vent length of approximately 520 mm. Thereafter females normally produce litters in alternate years. The number of young is roughly correlated with size of the female. In primiparae, litters of three are common (sometimes only one or two young are born) and the largest females frequently produce litters of eight or more (exceptionally 14). Courtship and copulation have rarely been observed, either in captivity or in nature. Presumably these activities are normally nocturnal. Cloacal smears from both sexes indicate that males almost always have motile sperm and that copulation may take place in any month throughout the snakes' season of activity. Perhaps copulation takes place most frequently in April soon after emergence from hibernation, and in the latter half of May, the season when ovulation occurs. The females carry their young throughout the summer. Gravid females sometimes gather in small groups. Births are concentrated in the first half of September but may occur in late August or early October. After insemination and fertilization of the mature ova, sperm may remain viable in the oviducts for at least a year and may fertilize the eggs for a subsequent litter of young. At birth the sex ratio is remarkably unbalanced, with males outnumbering females by more than three to one. In gravid females that are undernourished, some of the embryos are aborted or resorbed; other embryos, although stunted, survive, and are born as much undersized young after an abnormally prolonged gestation. In many instances such stunted young were known to have lived to become normal adults.

Normal young are in the neighborhood of 220 mm. in length from snout to vent, and twelve grams at birth, and the males and females are not noticeably different in size or proportions. The young differ from adults in the conspicuously yellow-tipped tail, a feature shared by the young of other members of the genus. Behavior suggesting the luring of prey within range, by squirming movements of the erect and conspicuous yellow tail, has been reported in young copperheads, but this behavior is much more strongly developed in their congeners the cantil, and the hump-nosed viper of India.

Young copperheads grow most rapidly in their first two years and there is but little divergence between the sexes during this time. In the third year growth rate slows a little in the males and much more in the females. Typical snout-vent lengths for males one, two, three, four, five, six, and seven years old are, respectively, 354, 480, 560, 620, 668, 710 and 760 mm. Corresponding measurements for females are: 345, 450, 538, 578, 598, 626 and 643 mm. Copperheads that are fully adult may continue to grow for many years but the rate is variable and erratic. Unusually large individuals of either sex are almost always more than seven years old, but the oldest individuals are not necessarily the largest.

The food consists of small vertebrates and certain insects, notably cicadas and the larvae of large moths of several families. In the food of the adult snakes, voles (especially *Microtus*), mice (especially *Peromyscus*), and shrews (especially *Blarina*) are most important, in that order of frequency. The young, still too small to prey freely on these animals, more often take small snakes, lizards, least shrews (*Cryptotis*), and narrow-mouthed toads (*Gastrophryne*). Frogs and toads (other than *Gastrophryne*) are rarely eaten by copperheads of the local population studied; published reports indicate that in some other regions frogs are more important in the diet. Various birds are eaten occasionally but they comprise an insignificant percentage of the food. Exceptional items eaten include young turtles (*Terrapene, Sternothaerus*), a mantis, and spiders.

In summer approximately half of the copperheads caught had food remains in their digestive tracts, but only eight per cent had food in their stomachs. Because the traps were selective, catching chiefly the more active and hungry snakes, the figures are biased. Other workers, obtaining copperheads by techniques that did not include trapping, have found food remains in the digestive tracts of approximately 73 per cent of a combined sample of 249. A meal of average size (18.5 per cent of the snake's body weight) remains in the stomach three to five days before it passes into the intestine in a semi-liquefied state. Residues often remain in the intestine for as much as two weeks before evacuation. It is estimated that a typical copperhead consumes eight meals totalling approximately twice its own bodily weight in the course of a growing season.

Presumably hundreds of copperheads die each year on the Reservation in the course of normal turnover of the population, but the causes of most of this mortality remain obscure. In three instances opossums were known to have fed upon copperheads, which the opossums may have killed. Experimental evidence bore out the suspicion that the mole may on occasion attack and kill juveniles. Other kinds of snakes including, among local species, the yellow-bellied racer and the common garter snake, sometimes prey upon young copperheads. Published records indicate that the common king snake is a natural enemy of major importance in some regions where it is abundant. Among the larger predators of the Reservation, whose food habits have been investigated, the red-tailed hawk stands out as by far the most important predator on the copperhead. A total of 224 pellets of red-tailed hawks analyzed included 40 occurrences of the copperhead. An effect of a rare extreme of weather was observed at Independence Creek, Terrell County, Texas, where, in June, 1954, a hurricane with rainfall allegedly in excess of 20 inches resulted in flooding that destroyed most of the live-oak groves that were the copperhead's habitat locally. Four species of chiggers are common ectoparasites of the copperhead on the Reservation. Other known parasites include a fluke (*Renifer kansensis*), and nematodes (*Kalicephalus agkistrodontis* and *Physaloptera squamatae*). In the copperheads examined, evidence of disease was noted from time to time and especially in the summers of 1950 and 1951. In those years many individuals had necrotic patches of skin, and some were emaciated.

The breeding population contains a tremendous excess of males because they are more numerous at birth and attain breeding maturity much sooner. Regardless of the method of collecting, the young up to two years old are not represented in their true numbers. An annual loss close to 29 per cent in the population as a whole is indicated. In the young the mortality is a little higher than this and in the large adults it is a little less. Because of the long time required to collect a sample on any area and the impossibility of finding all individuals, any attempt at census must be based upon the ratio of marked individuals, and must make allowance for the rate of population turnover, with compensation for immigration, emigration, natality and mortality. Extent of normal movements and frequency of shifts are still inadequately known for a highly accurate census. Many different census computations were made, using different combinations of samples. The figures obtained varied over a wide range, perhaps reflecting actual changes in population density from time to time and from place to place, but probably reflecting, to a greater extent, inadequacies in the samples, resulting from small numbers or from sources of error inherent in the method. Allowing for the probable errors produced by population turnover, it is conservatively estimated that the population on the Reservation in autumn after birth of the young slightly exceeds five per acre. No comparable data are available from any other area. Judging from the relative ease with which individuals are found by turning flat rocks in spring, the population density of the Reservation is fairly typical of other areas in northeastern Kansas having similarly favorable combinations of habitat features including woodland, meadow, brush, and south-facing exposures of fissured rock that crop out near the tops of hills. Certainly many areas within Douglas County and the counties adjoining it, have much higher population densities, probably exceeding ten per acre.

The copperhead is to some extent hated and feared by the human population throughout its range. It is feared most where it is rare and is generally unfamiliar except as a mental image far more fearsome than the snake itself. Where the species is common, it is often accepted casually, and is feared less than some harmless snakes of more striking appearance and aggressive demeanor, which are believed to be dangerous. In the region of this study, irresponsible journalism by local newspapers has done much in recent years to promote a dread of snakes by less well-informed segments of the public. Incidents involving venomous or supposedly venomous snakes are mentioned frequently by the press, almost always in a context of sensationalism, with gross exaggeration of size, venomous qualities and aggressiveness.

Because of its small size, sluggish and secretive and nocturnal habits, and highly developed cryptic coloration, the copperhead has survived in areas densely populated with humans, even in the suburbs of large cities. Where it is abundant in such situations, it may constitute a hazard to small children, and should be controlled locally. Recommended control measures include removal or reduction of the available food and shelter, and heavy spraying in spring and fall, with concentrated solutions of insecticides at the crevices and fissures in rock outcrops where the snakes are known to hibernate.

The sluggish habits and cryptic coloration are correlated with the development of venom glands and fangs for subduing the prey. In the United States the copperhead inflicts more bites on humans than does any other species of venomous snake, but the incidence of mortality is low. Even in untreated cases, victims other than small children are almost certain to recover unless there are seriously aggravating circumstances. The venom of individual copperheads varies greatly and unpredictably both in quantity and in the potency of any given amount. Compared with the venoms of most rattlesnakes, of the cottonmouth, and of the Neotropical pit vipers, that of the copperhead is much less potent in its effect on humans, in a subcutaneous injection such as results from a typical bite, and is relatively strong in neurotoxic effects but causes less destruction of tissues. Grave sequelae, such as development of gangrene are comparatively rare. Most rattlesnakes have venoms two to six times as potent as that of the copperhead judging from the lethal doses required for mice; the venom of the South American rattlesnake is recorded to be 55 times as potent. Such comparisons are somewhat misleading and perhaps do not do justice to the copperhead. The venom kills in different ways according to the amount: by massive clotting and stoppage of circulation; by paralysis interfering with respiration; by gradual but cumulative damage to any one of several vital organs; or secondarily by septicemia, gas gangrene, or other infections. The more recent improved antivenin serum manufactured and distributed by Wyeth Laboratories, Inc., is obtained from horses injected with a combination of *Bothrops* and *Crotalus* venoms of four species. Although no venom of *Agkistrodon* is used in its preparation, this new serum is found to be more effective against the bite of the copperhead than the original antivenin which did rely in part on the venom of the copperhead. Formerly popular methods of treatment of snakebite—such as holding the raw flesh of a freshly killed fowl against the wound, treating the wound with kerosene, or with solution of potassium permanganate, cryotherapy, or imbibing of liquor—are all now in disrepute. Recently some authorities have expressed the opinion that use of antivenin is not justified for treatment of the bites of copperheads, because of the risk of untoward reactions from the serum, and because the venom is so weak that recovery is virtually assured without the aid of the serum. Other recent workers have presented evidence that the long-established treatments by use of a tourniquet to impede the spread of venom, combined with incision and suction to remove it, are more harmful than beneficial, and that the early use of antivenin is the only effective method of treatment.

Compared with other vertebrates of similar size, snakes in general are more resistant to snake venoms. The copperhead is more than normally susceptible to the venom of its own species, and in captivity one may occasionally be killed by a well-placed bite. Such occurrences are accidental, and so far as known the venom normally is used only to secure the prey or, secondarily, in defense against natural enemies.

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28-4428

(Continued from inside of front cover)

Vol. 8. 1. Life history and ecology of the five-lined skink, Eumeces fasciatus. By Henry S. Fitch. Pp. 1-156, 26 figures in text. September 1, 1954.

2. Myology and serology of the Avian Family Fringillidae, a taxonomic study. By William B. Stallcup. Pp. 157-211, 23 figures in text, 4 tables. November 15, 1954.

3. An ecological study of the collared lizard (Crotaphytus collaris). By Henry S. Fitch. Pp. 213-274, 10 figures in text. February 10, 1956.

4. A field study of the Kansas ant-eating frog, Gastrophryne olivacea. By Henry S. Fitch. Pp. 275-306, 9 figures in text. February 10, 1956.

5. Check-list of the birds of Kansas. By Harrison B. Tordoff. Pp. 307-359, 1 figure in text. March 10, 1956.

6. A population study of the prairie vole (Microtus ochrogaster) in northeastern Kansas. By Edwin P. Martin. Pp. 361-416, 19 figures in text. April 2, 1956.

7. Temperature responses in free-living amphibians and reptiles of northeastern Kansas. By Henry S. Fitch. Pp. 417-476, 10 figures in text, 6 tables. June 1, 1956.

8. Food of the crow, Corvus brachyrhynchos Brehm, in south-central Kansas. By Dwight Platt. Pp. 477-498, 4 tables. June 8, 1956.

9. Ecological observations on the woodrat Neotoma floridana. By Henry S. Fitch and Dennis G. Rainey. Pp. 499-533, 3 figures in text. June 12, 1956.

10. Eastern woodrat, Neotoma floridana: Life history and ecology. By Dennis G. Rainey. Pp. 535-646, 12 plates, 13 figures in text. August 15, 1956.

Index. Pp. 647-675.

Vol. 9. 1. Speciation of the wandering shrew. By James S. Findley. Pp. 1-68, 18 figures in text. December 10, 1955.

2. Additional records and extension of ranges of mammals from Utah. By Stephen D. Durrant, M. Raymond Lee, and Richard M. Hansen. Pp. 69-80. December 10, 1955.

3. A new long-eared myotis (Myotis evotis) from northeastern Mexico. By Rollin H. Baker and Howard J. Stains. Pp. 81-84. December 10, 1955.

4. Subspeciation in the meadow mouse, Microtus pennsylvanicus, in Wyoming. By Sydney Anderson. Pp. 85-104, 2 figures in text. May 10, 1956.

5. The condylarth genus Ellipsodon. By Robert W. Wilson. Pp. 105-116, 6 figures in text. May 19, 1956.

6. Additional remains of the multituberculate genus Eucosmodon. By Robert W. Wilson. Pp. 117-123, 10 figures in text. May 19, 1956.

7. Mammals of Coahuila, Mexico. By Rollin H. Baker. Pp. 125-335, 75 figures in text. June 15, 1956.

8. Comments on the taxonomic status of Apodemus peninsulae, with description of a new subspecies from North China. By J. Knox Jones, Jr. Pp. 337-346, 1 figure in text, 1 table. August 15, 1956.

9. Extensions of known ranges of Mexican bats. By Sydney Anderson. Pp. 347-351. August 15, 1956.

10. A new bat (Genus Leptonycteris) from Coahuila. By Howard J. Stains. Pp. 353-356. January 21, 1957.

11. A new species of pocket gopher (Genus Pappogeomys) from Jalisco, Mexico. By Robert J. Russell. Pp. 357-361. January 21, 1957.

12. Geographic variation in the pocket gopher, Thomomys bottae, in Colorado. By Phillip M. Youngman. Pp. 363-387, 7 figures in text. February 21, 1958.

13. New bog lemming (genus Synaptomys) from Nebraska. By J. Knox Jones, Jr. Pp. 385-388. May 12, 1958.

14. Pleistocene bats from San Josecito Cave, Nuevo León, México. By J. Knox Jones, Jr. Pp. 389-396. December 19, 1958.

15. New subspecies of the rodent Baiomys from Central America. By Robert L. Packard. Pp. 397-404. December 19, 1958.

16. Mammals of the Grand Mesa, Colorado. By Sydney Anderson. Pp. 405-414, 1 figure in text, May 20, 1959.

17. Distribution, variation, and relationships of the montane vole, Microtus montanus. By Sydney Anderson. Pp. 415-511, 12 figures in text, 2 tables. August 1, 1959.

18. Conspecificity of two pocket mice, Perognathus goldmani and P. artus. By E. Raymond Hall and Marilyn Bailey Ogilvie. Pp. 513-518, 1 map. January 14, 1960.

19. Records of harvest mice, Reithrodontomys, from Central America, with description of a new subspecies from Nicaragua. By Sydney Anderson and J. Knox Jones, Jr. Pp. 519-529. January 14, 1960.

20. Small carnivores from San Josecito Cave (Pleistocene), Nuevo León, México. By E. Raymond Hall. Pp. 531-538, 1 figure in text. January 14, 1960.

21. Pleistocene pocket gophers from San Josecito Cave, Nuevo León, México. By Robert J. Russell. Pp. 539-548, 1 figure in text. January 14, 1960.

(Continued on outside of back cover)

(Continued from inside of back cover)

22. Review of the insectivores of Korea. By J. Knox Jones, Jr., and David H. Johnson. Pp. 549-578. February 23, 1960.
23. Speciation and evolution of the pygmy mice, genus Baiomys. By Robert L. Packard. Pp. 579-670, 4 plates, 12 figures in text. June 16, 1960.

Index. Pp. 671-690.

Vol. 10. 1. Studies of birds killed in nocturnal migration. By Harrison B. Tordoff and Robert M. Mengel. Pp. 1-44, 6 figures in text, 2 tables. September 12, 1956.
2. Comparative breeding behavior of Ammospiza caudacuta and A. maritima. By Glen E. Woolfenden. Pp. 45-75, 6 plates, 1 figure. December 20, 1956.
3. The forest habitat of the University of Kansas Natural History Reservation. By Henry S. Fitch and Ronald R. McGregor. Pp. 77-127, 2 plates, 7 figures in text, 4 tables. December 31, 1956.
4. Aspects of reproduction and development in the prairie vole (Microtus ochrogaster). By Henry S. Fitch. Pp. 129-161, 8 figures in text, 4 tables. December 19, 1957.
5. Birds found on the Arctic slope of northern Alaska. By James W. Bee. Pp. 163-211, plates 9-10, 1 figure in text. March 12, 1958.
6. The wood rats of Colorado: distribution and ecology. By Robert B. Finley, Jr. Pp. 213-552, 34 plates, 8 figures in text, 35 tables. November 7, 1958.
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8. Natural history of the salamander, Aneides hardyi. By Richard F. Johnston and Gerhard A. Schad. Pp. 573-585. October 8, 1959.
9. A new subspecies of lizard, Cnemidophorus sacki, from Michoacán, México. By William E. Duellman, Pp. 587-598, 2 figures in text. May 2, 1960.
10. A taxonomic study of the Middle American Snake, Pituophis deppei. By William E. Duellman. Pp. 599-610, 1 plate, 1 figure in text. May 2, 1960.

Index. Pp. 611-626.

Vol. 11. 1. The systematic status of the colubrid snake, Leptodeira discolor Günther. By William E. Duellman. Pp. 1-9, 4 figures. July 14, 1958.
2. Natural history of the six-lined racerunner, Cnemidophorus sexlineatus. By Henry S. Fitch. Pp. 11-62, 9 figures, 9 tables. September 19, 1958.
3. Home ranges, territories, and seasonal movements of vertebrates of the Natural History Reservation. By Henry S. Fitch. Pp. 63-326, 6 plates, 24 figures in text, 3 tables. December 12, 1958.
4. A new snake of the genus Geophis from Chihuahua, Mexico. By John M. Legler. Pp. 327-334, 2 figures in text. January 28, 1959.
5. A new tortoise, genus Gopherus, from north-central Mexico. By John M. Legler. Pp. 335-343. April 24, 1959.
6. Fishes of Chautauqua, Cowley and Elk counties, Kansas. By Artie L. Metcalf. Pp. 345-400, 2 plates, 2 figures in text, 10 tables. May 6, 1959.
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9. Description of a new softshell turtle from the southeastern United States. By Robert G. Webb. Pp. 517-525, 2 plates, 1 figure in text. August 14, 1959.
10. Natural history of the ornate box turtle, Terrapene ornata ornata Agassiz. By John M. Legler. Pp. 527-669, 16 pls., 29 figures in text. March 7, 1960.

Index Pp. 671-703.

Vol. 12. 1. Functional morphology of three bats: Eumops, Myotis, Macrotus. By Terry A. Vaughan. Pp. 1-153, 4 plates, 24 figures in text. July 8, 1959.
2. The ancestry of modern Amphibia: a review of the evidence. By Theodore H. Eaton, Jr. Pp. 155-180, 10 figures in text. July 10, 1959.
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2. A distributional study of the amphibians of the Isthmus of Tehuantepec, México. By William E. Duellman. Pp. 19-72, pls. 1-8, 3 figures in text. August 16, 1960.
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Introduction

The common garter snake (*Thamnophis sirtalis*) has by far the most extensive geographic range of any North American reptile, covering most of the continental United States from the Atlantic to the Pacific and from south of the Mexican boundary far north into Canada and southeastern Alaska. Of the several recognized subspecies, the eastern *T. s. sirtalis* has the most extensive range, but that of *T. s. parietalis* in the region between the Mississippi River and the Rocky Mountains is almost as large. The more western *T. s. fitchi* occurring from the Oregon and California coasts east through the northern Great Basin, has the third largest range, while the far western subspecies *pickeringi, concinnus, infernalis* and *tetrataenia,* and the Texan *T. s. annectens* all have relatively small ranges.

Since the publication of Ruthven's revision of the genus *Thamnophis* more than 50 years ago, little attention has been devoted to the study of this widespread and variable species, except in the Pacific Coast states (Van Denburgh, 1918; Fitch, 1941; Fox, 1951). However, Brown (1950) described the new subspecies *annectens* in eastern Texas, and many local studies have helped to clarify the distribution of the species in the eastern part of the continent and to define the zone of intergradation between the subspecies *sirtalis* and *parietalis.* In our study attention has been focused upon *parietalis* in an attempt to determine its western limits and its relationships to the subspecies that replace it farther west.

Taxonomic History

Thamnophis sirtalis parietalis Say was described (as *Coluber parietalis*) in 1823 from a specimen obtained in what is now Washington County, Nebraska, on the west side of the Missouri River three miles upstream from the mouth of Boyer's River [Iowa], or approximately eight miles north of Omaha. Although the type locality was unequivocally stated in the original description, Nebraska was not mentioned since the state was not yet in existence. Because the mouth of Boyer's River, the landmark by means of which the type locality is defined, is in Iowa, the impression has been imparted that the type locality itself is in Iowa (Schmidt, 1953:175), and to our knowledge the type locality has never been associated with Nebraska in the literature.

Like all the more western subspecies, *parietalis* is strikingly different from typical *sirtalis* in having conspicuous red markings. The relationship between the two was early recognized. Several of the other subspecies were originally described as distinct species. *Coluber infernalis* Blainville, 1835; *Tropidonotus concinnus* Hallowell, 1852; *Eutainia pickeringi* Baird and Girard, 1853; and others now considered synonyms eventually came to be recognized as conspecific with *Thamnophis sirtalis.* Ruthven (1908:166-173) allocated all western *sirtalis* to either *parietalis* or *concinnus*, the latter including the populations of the northwest coast in Oregon, Washington and British Columbia.

Subsequent more detailed studies by later workers with more abundant material led to the recognition of some subspecies that Ruthven thought invalid and led to the resurrection of some names that he had placed in synonomy. Van Denburgh and Slevin (1918: 198) recognized *infernalis* as the subspecies occurring over most of California and southern Oregon, differing from more northern populations in having more numerous ventrals and caudals and a paler ground color. Fitch (1941:575) revived the name *pickeringii* for a melanistic population of western Washington and southwestern British Columbia, restricting the name *concinnus* to a red-headed and melanistic population of northwestern Oregon, and restricting the name *infernalis* to a pale-colored population in the coastal strip of California.

These changes left most of the populations formerly included in *concinnus* and *infernalis* without a name, and Fitch (*op. cit.*) revived *Thamnophis sirtalis tetrataenia* (Cope) to apply to them. However, Fox (1951:257) demonstrated that the type of *T. s. tetrataenia* came from the San Francisco peninsula (rather than from "Pit River, California" as erroneously stated in the original description) and that the name was applicable to a localized peninsular population rather than to the wide-ranging far western subspecies, which he named *T. s. fitchi.* The range of *fitchi* includes California west of the Colorado and Mohave deserts (except for the narrow strip of coast occupied by *infernalis* and *tetrataenia*), Oregon except the northwestern part, Washington east of the Cascade Range, most of British Columbia, extreme southeastern Alaska (occurring farther north than any other terrestrial reptile of North America) and parts of Idaho.

Neither Fox (1951) nor Fitch (1941) defined the eastern limits of *fitchi* or discussed its relationship to the subspecies *parietalis.* Wright and Wright (1957:849) stated: "Fitch . . . did not even mention the big scrap basket form *parietalis,* from which he pulled *T. s. fitchi* (old *tetrataenia*). That comparison remains to be made, and the east boundary of *fitchi* and the west boundary of *parietalis* are still nebulous." We have undertaken to define better than has been done before the ranges of *parietalis* and *fitchi* and to list the diagnostic characters separating these two subspecies. Freshly collected material of both has been compared. At the time of his 1941 revision the senior author had never seen a live or recently preserved specimen of *parietalis.*

Discontinuity of Range

Wherever it occurs at all, the common garter snake is usually abundant. Because of its diurnal habits and the concentration of its populations along watercourses, it is not likely to be overlooked. There are few, if any, remaining large areas in the United States where herpetologists have not carried on field work. It may be anticipated that certain rare and secretive species will still be found far from any known stations of occurrence, and seeming gaps in the ranges of these species will eventually be filled. But for the common garter snake the negative evidence provided by the lack of records from extensive areas should be taken into account in mapping the range.

Most large collections of garter snakes contain misidentified specimens. The diagnostic differences in color and pattern are often obscured, especially if the specimens are poorly preserved. Many specimens deviate from the scalation typical of the form they represent, and key out to other species. Isolated records should therefore be accepted with caution. A case in point is Colorado University Museum No. 46, from Buford, Rio Blanco County, Colorado, originally identified by Cockerell (1910:131) as *Thamnophis sirtalis parietalis.* This specimen, and another, now lost, from Meeker in the same county seemingly served as the basis for mapping the range of *sirtalis* across the western half of Colorado, for there seem to be no other records from this part of the state. However, a re-examination of the specimen from Buford shows it to be an atypical individual of another species, *T. elegans vagrans.* A specimen of *T. radix haydeni* (Col. U. Mus. No. 3165) was the basis for Maslin's (1959:53) record of *parietalis* in Baca County on the north fork of the Cimarron River in southeastern Colorado. Brown (1950:203) has mentioned the difficulty of defining the range of *sirtalis* in the southern Great Plains because of misidentifications of the similar *T. radix.*

The range of the common garter snake has never been adequately mapped in the Rocky Mountain and Great Basin states. Recent general works (Smith, 1956:291; Wright and Wright 1957:834; Stebbins 1954:505; Conant 1958:328) which have shown maps of the over-all range of *sirtalis,* differ sharply as to the extent of its distribution in Texas, New Mexico and Arizona, but all show its distribution as continuous over the more northern Great Basin and Rocky Mountain states. However, specimens and specific locality records from this extensive area seem to be scarce and some are based on early collections of doubtful provenance. Throughout this region the low rainfall, fluctuating and uncertain water supply, and general lack of mesic vegetation along many of the streams render the habitat rather hostile to garter snakes in general. *Thamnophis elegans vagrans,* highly adapted to conditions in this region and generally distributed over it, doubtless offers intensive competition to the species *sirtalis* wherever they overlap and perhaps constitutes a limiting factor for *sirtalis* in some drainage basins.

Convincing records of *sirtalis* are lacking from all of Colorado—except for those in the drainage basins of the South Platte, and the Río Grande east of the Continental Divide—from the eastern half of Utah (east of the Wasatch Range), from New Mexico except for the Río Grande drainage (with one record each for the Canadian and Pecos river drainages), from southwestern Wyoming (at least that part in the Colorado River drainage basin), from the western half of Oklahoma, and from Texas, except the eastern and extreme western and northern parts. The species occurs in Nevada only near that state's western and northern boundaries. The range is therefore much different than it has been depicted heretofore, with the populations living east of the Continental Divide widely separated from those to the west for the entire length of the Rocky Mountains south of the Yellowstone National Park region. The populations of northern Utah, southern Idaho, and Nevada, which have been considered *parietalis* are thus far removed from the main population of that subspecies to the east and are isolated from them by the barrier of the Continental Divide and arid regions farther west.

Although some of the records published for *Thamnophis sirtalis* are erroneous, being based on misidentifications of other species, various outlying records, including those in western Kansas, the Panhandle of Texas, and southeastern New Mexico probably represent localized relict populations that have survived from a time when the species was more generally distributed in this region. The population of *T. sirtalis* in the Río Grande drainage of New Mexico is geographically isolated and remote from other populations of the species. Except for a few isolated and highly localized populations the species is absent from the Republican, Smoky Hill, Arkansas, Cimarron, Canadian, Red, Brazos, Colorado and Pecos rivers and their tributaries west of the one hundredth meridian in the arid High Plains.

Streams in this region of High Plains are in most instances unsuitable habitats because they are in eroded channels, have a variable and uncertain water supply, and have poorly developed riparian communities. The marsh and wet meadow habitat preferred by *sirtalis* in most parts of its range is almost absent. *T. radix* and *T. marcianus,* well adapted to conditions in this region, perhaps provide competition that is limiting to *T. sirtalis.* However, several well-isolated populations of *sirtalis* have survived as relicts in the southern Great Plains, presumably from a time several thousand years ago when mesic conditions were more prevalent, perhaps in an early postglacial stage.

Smith (1956:292) recorded *parietalis* from three outlying stations in the western quarter of Kansas, from Wallace, Hamilton and Meade counties in the drainages of the Smoky Hill River, Arkansas River, and Cimarron River, respectively. Permanent springs in Meade County State Park perhaps account for the survival of an isolated colony there. Several specimens from that locality seen by Fitch in August, 1960, when recently collected by a University of Michigan field party, seemed to be of the Texas subspecies *annectens,* as their dorsal stripes were reddish orange, and markings on the dorsolateral area were pale yellow rather than red. Specimens from the Texas Panhandle, from Hemphill County (Brown, 1950: 207) and nine miles east of Stinnet, Hutchison County (Fouquette and Lindsay, 1955:417) likewise are most nearly like *annectens* judging from the authors' descriptions. The specimens from nine miles east of Stinnet averaged large; the two largest would have attained or slightly exceeded four feet in length if they had had com-

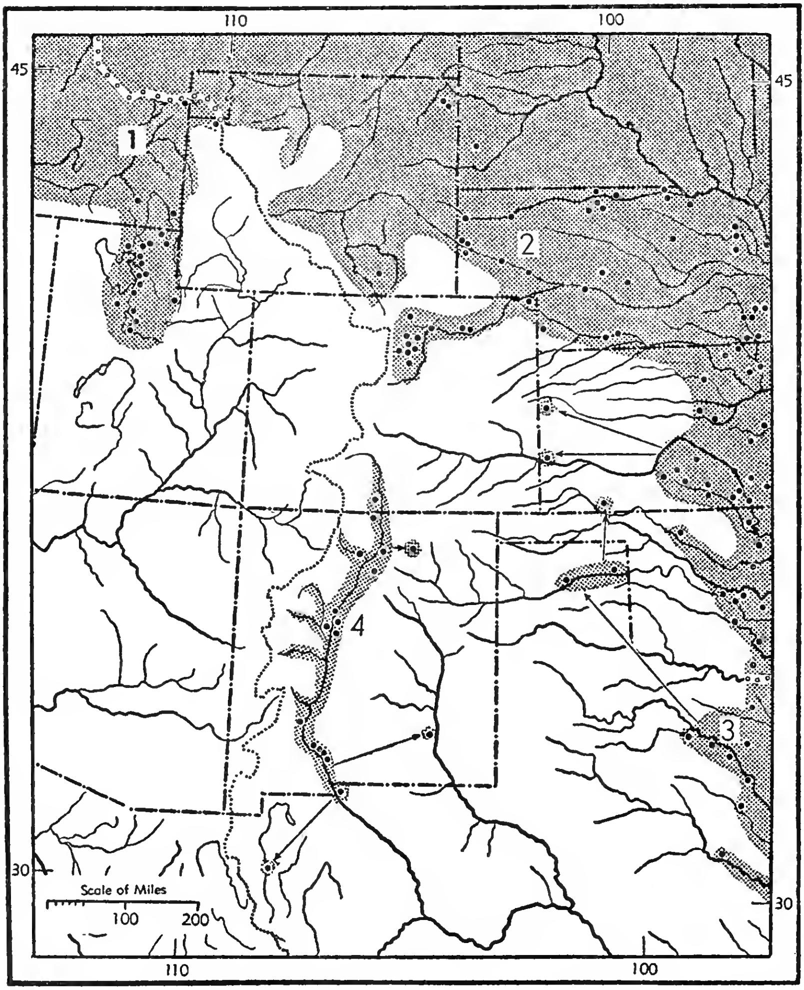

FIG. 1. Map of a part of the United States in the region of the Great Plains and Rocky Mountains, and adjacent northwestern Mexico showing supposed range (shaded) and localities of authenticated occurrence (dots) of *Thamnophis sirtalis*. 1. *T. s. fitchi*, 2. *T. s. parietalis*, 3. *T. s. annectens*, 4. *T. s. ornata*. Records from Idaho and Wyoming are based on specimens in the University of Kansas Museum of Natural History collection. Other records are based on Woodbury (1931) for Utah, Hudson (1942) for Nebraska, Maslin (1959) for Colorado, Smith (1956) for Kansas, R. G. Webb (MS) for Oklahoma, Brown (1950) and Fouquette and Lindsay (1955) for Texas, Cope (1900), Van Denburgh (1924), Little and Keller (1937) for New Mexico, and Smith and Taylor (1945) for Mexico.

plete tails. No *sirtalis* so long as four feet has been recorded elsewhere.

Records are lacking from the drainages of the Republican, North Canadian, Brazos and Colorado River drainages in the High Plains, but possibly isolated populations occur in some of these also. The only record from the Pecos River drainage is that of Bundy (1951: 314) from Wade's Swamp near Artesia, Eddy County, New Mexico. This locality is separated by some 140 miles from any other known station of occurrence.

From extreme southern Colorado south across New Mexico to the Mexican border *T. sirtalis* occurs in continuous or nearly continuous populations in the Río Grande Valley, and has been recorded from many localities. It has been recorded from relatively few localities of tributary streams (Los Pinos, Abiqui, Santa Fe) all near the main valley. There is one record from the Ocate River, a headwaters tributary of the Canadian River, in the Sangre de Cristo Mountains near other localities in the Río Grande drainage. The southwesternmost known locality of occurrence is Casas Grandes in the Mexican state of Chihuahua some 130 miles southwest of El Paso, Texas, and near the Continental Divide. The Río Casas Grandes must have once been a tributary of the Río Grande, but now its desert drainage basin is isolated.

Re-description of a Subspecies from New Mexico

Most specimens of a population of *sirtalis* occurring in New Mexico are recognizably different from most specimens of other populations. This New Mexican population is therefore here recognized as a distinct subspecies:

Thamnophis sirtalis ornata Baird

Eutaenia ornata Baird, 1859:16.
Eutaenia sirtalis dorsalis Cope, 1900:1076.
Thamnophis sirtalis parietalis (part) Van Denburgh, 1924:222.

Type.—U. S. Nat. Mus. No. 960, obtained at El Paso, Texas, at some time in the eighteen fifties by Col. J. D. Graham.

Range.—Río Grande and vicinity, from Conejos and Costilla counties in extreme south-central Colorado south across New Mexico to Mexican border. Records from neighboring drainage systems, Casas Grandes in Chihuahua and Artesia and Ocate River in New Mexico, probably also pertain to *ornata*.

Description.—A specimen in the University of New Mexico Natural History Museum (E. D. Flaherty No. 560, obtained one mile west and one-half mile south of Isleta, Bernalillo County, New Mexico, on May 31, 1959) was described as follows while its colors were still but little altered by preservatives: Top of head olive, supralabials pale gray, edged with black posteriorly; chin milky white, with dark edges posteriorly on fifth, sixth and seventh infralabials;

dorsal stripe yellow; including middorsal row of scales and little more than adjacent half of row on either side of it; dorsolateral area olive-brown with row of black spots on its lower half, these spots elliptical, averaging about size of one scale on anterior part of body, smaller posteriorly; adjacent spots separated by interspaces of approximately their own length, irregular black markings on upper half of dorsolateral area not forming definite spots but fused longitudinally to form continuous black border to dorsal stripe; crescent-shaped red markings in areas between scale rows three to nine, these markings invading edges of scales, and themselves having ill-defined edges blending into the darker ground color; lateral stripe pale, yellowish gray, limited to scale rows two and three for most of its length, but including rows four and five in neck region; row of irregular black marks low on each side, with each mark centering on anterior part of lower half of scale of first row but overlapping onto corners of adjacent ventrals; approximately every other scale of first row so marked; ventral surface pale, suffused with bluish tint; most of ventrals marked on anterior edges with pair of semicircular black spots, each situated about two-thirds of distance from midline to lateral edge of ventral; these marks diminishing in size and finally disappearing on posterior part of body; ventral surface otherwise immaculate.

Lepidosis normal for genus and species, with preoculars single on each side, supralabials 7-7, infralabials 8-8, ventrals 159, anal entire, subcaudals 77 (including terminal spine), paired except for second, third and fourth; scale rows 19 from neck slightly beyond mid-body, fifth on left side ending opposite 86th ventral; length from snout to vent 670 mm., tail 202 mm.

Comparisons.—From *T. s. parietalis, T. s. ornata* differs in its consistently pale ground color, olive instead of dark brown or black. In respect to color-pattern *ornata* stands in approximately the same relation to *parietalis* as, farther west, *T. s. infernalis,* a pale subspecies of the California coast, stands in relation to *T. s. fitchi.* Nevertheless, *fitchi* consistently has a dark ground color, whereas *parietalis* is highly variable, and the color of an occasional specimen (for example KU 17032 from Douglas County, Kansas) matches *ornata* in olive coloration. These unusually pale specimens of *parietalis* differ from *ornata* in not having a continuous black edge along each side of dorsal stripe; black pigment of this area is concentrated into rows of spots alternating with those of lower series. From *T. s. infernalis, ornata* differs in having paired black spots on the ventrals and in having more than three series of red crescents on dorsolateral area of each side.

Remarks.—The type of *ornata* seems to have been lost, and the available information concerning it is far from satisfactory. In the original description, Baird listed three specimens, purportedly from "Indianola, Texas" (J. H. Clark, 438), from the Río Grande, Texas (J. H. Clark, 768), and from near San Antonio, Texas (Dr. Kennerley, no number). None of these three specimens could have been *ornata* as conceived of by us because all were collected outside the geographic range of *ornata.* However, there was also included a plate with a drawing of a specimen and a reference to an earlier paper (Baird and Girard, 1853) in which a specimen obtained by Col. Graham "Between San Antonio and El Paso" was described. Smith and Brown (1946:72) have presented evidence that this specimen figured (rather than any of the three specifically mentioned) served as a basis for the plate, and they therefore considered it to be the holotype of *ornata*, even though Baird referred this specimen to "*Eutaenia parietalis* Say" in the same paper (1859) in which the original description of *ornata* was published. Cope (1900:1079) listed under *Eutaenia sirtalis parietalis* a specimen, U. S. Nat. Mus. No. 960, from El Paso, obtained by Col. Graham, and referred to it as a type (without specifying of what it was the type). Smith and Brown (*loc. cit.*) interpreted this statement by Cope as further evidence that the specimen in question should be considered the type of *ornata*, and they restricted the type locality, originally stated as "between San Antonio and El Paso" to "El Paso." Actually all valid records of the species *sirtalis* from the vicinity of the Río Grande are from the El Paso region or from farther north.

It is with some misgivings that we herewith accept the interpretation proposed by Smith and Brown regarding the applicability of the name *ornata* and the designation by these authors of the now missing specimen from the region of El Paso as the holotype of that form. The evidence linking the name *ornata* with the New Mexican subspecies is tenuous; there is some doubt as to the provenance of U. S. Nat. Mus. No. 960 (the supposed type), and even more doubt as to whether this is the specimen depicted in the plate that formed part of the original description.

Cope (1900:1076) recognized as a distinct subspecies, *Eutaenia sirtalis dorsalis*, the same population that we recognize herein as *T. s. ornata*, and Smith (1942:98) considered the name *dorsalis* to be a synonym of *T. s. parietalis*. However, it is almost certain that both authors misapplied the name, since the type of Baird's and Girard's (1853:31) *Eutainia dorsalis* was obtained in Coahuila, Mexico, between Monclova and the Río Grande, far south of the known range limits of *T. sirtalis* in Texas. The description does not fit *T. sirtalis* and almost certainly pertains to another species.

Specimens examined.—Univ. of Kansas Mus. Nat. Hist. (hereafter abbreviated to "KU") Nos. 5479 to 5497, from the north end of Elephant Butte Reservoir, Sierra County, New Mexico, and 8592 and 8593 from near Las Lunas, Valencia County, New Mexico; Univ. of New Mexico Mus. Nos. 571 and 572 (J. S. Findley) from 2 miles west and ¼ mile north of Albuquerque, Bernalillo County, New Mexico, and No. 4021 (E. D. Flaherty) from 1 mile west and ½ mile south of Isleta, Bernalillo County, New Mexico.

Description of *T. s. parietalis*

From most of the vast area occupied by *parietalis*, material has not been available to us, and our concept of this subspecies is based chiefly on specimens and living material from Kansas and northeastern Colorado. A total of 520 live *parietalis* has been examined from the University of Kansas Natural History Reservation some 130 miles south and a little east of the type locality in Nebraska. These probably differ but little from typical specimens. The range of individual variation in pattern is especially notable. In those from the Reservation, the ground color varies from dull olive-brown to almost jet black. The markings on the dorsolateral area vary in color, in shade and in extent. These marks are chiefly confined to the skin between the scales of rows three to nine. Although most typically these marks are of some shade of red (hence the name "red-sided garter snake"), they may be pale buff, or pale greenish yellow, or may even have a bluish tint. In approximately ten per cent of the specimens from the Reservation there is no red at all in the pattern, which hence is similar to that of *T. s. sirtalis* in the eastern United States. Only a minority have all the dorsolateral marks red, and in some of these specimens the marks higher on the sides are progressively paler red, having a bleached out appearance. Most typically the marks between rows three to six are some shade of red while the smaller marks between rows six to nine are pale—yellowish, greenish, or buffy. In some the pale area of the lateral stripe is in varying degrees suffused with red, which may extend onto the edges of the ventrals and even to the underside of the tail.

T. s. parietalis may be diagnosed, on the basis of these snakes from northeastern Kansas, as follows: Size medium large (length 23.5 to 34.5, or, exceptionally 43.5 inches in adult males; 32.5 to 46.0 inches in adult females), dorsolateral color olive to black. Approximately every other scale of the third row is bordered above and anteriorly by a crescent-shaped area of scarlet colored skin. Similar crescent-shaped areas border the scales of the fourth and fifth rows and often two adjacent crescents meet at the ends of an intervening scale and fuse forming an H-shaped mark. Placed alternately with these markings are similar but smaller crescent-shaped markings on the skin of the upper half of the dorsolateral area on each side bordering every other scale of the sixth, seventh and eighth rows. The crescents of this upper series also may fuse to form series of H-shaped markings alternating with those of the lower series. The dorsal stripe is yellow with a faint dusky suffusion; it involves all of the middorsal scale row and approximately the adjacent half of the row on either side. The lateral stripe is faint, yellowish gray, chiefly on the upper half of the second scale row, lower half of third, and the intervening skin, and is often invaded or suffused by the red marks of the dorsolateral area. The first scale row, adjacent corners of the ventrals, and lower half of the second scale row are suffused with dark pigment and appear dusky, but this area is often marked with black, setting off the paler area of the lateral stripe. The ventrals are dull, whitish, faintly suffused with yellowish, greenish or bluish, each ventral having a black dot usually of semicircular shape on its anterior margin near the anterolateral corner.

Comparison of *T. s. parietalis* and *T. s. fitchi*

Like most widely ranging subspecies, *parietalis* and *fitchi* vary geographically and local populations often are noticeably different from typical material. It is possible that future revisors will recognize additional subspecies, but in the variant populations known to us the degree of differentiation is slight as compared, for instance, with that in the subspecies of *Thamnophis elegans*. Scalation is remarkably uniform in all the subspecies of *sirtalis*, but coastal and northern populations tend to have fewer ventrals and subcaudals than do their counterparts farther inland and farther south. In their geographic variation the ventrals and subcaudals follow clines, and do not in themselves warrant subspecific divisions. Variation occurs chiefly in the color and pattern including the intensity of dark pigmentation of the dorsolateral area, head, ventral surface and lower edge of the lateral stripe; in extent, position and shade of red or pale colored markings on the dorsolateral area; in presence and extent of reddish suffusion on the head, in the region of the lateral stripe, and on the ventral surface of the tail. Most of these same characters

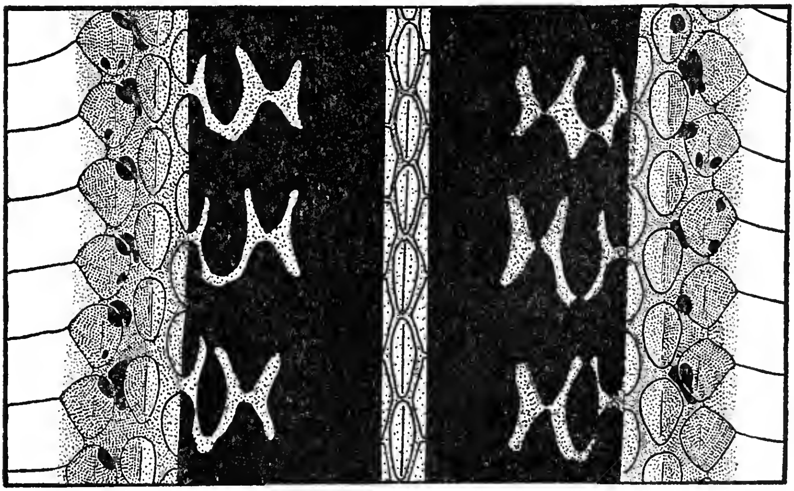

FIG. 2. Diagrammatic drawing of pattern in stretched skin of *T. s. fitchi;* the pale markings on the black dorsolateral area are scarlet (× 2¼).

vary within the subspecies *fitchi*, but the range of variation is relatively minor. Fitch (*op. cit.*:582-584) described typical populations and also described briefly several small series from British Columbia, Idaho, Oregon, and California which were not entirely typical. Most

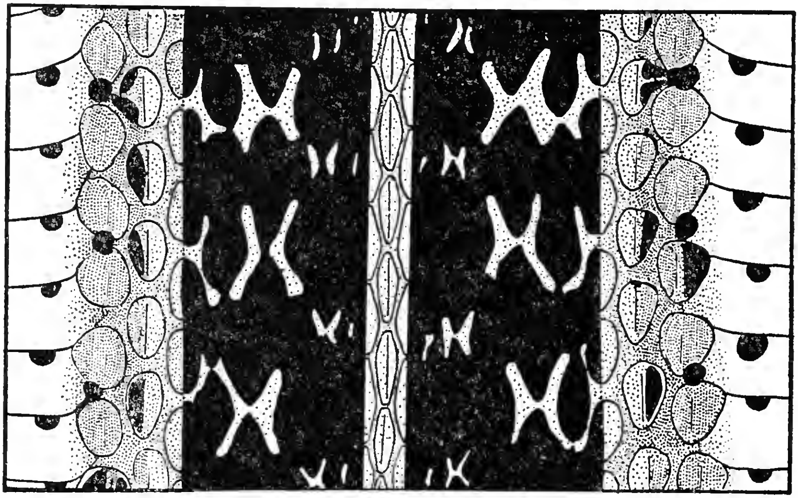

FIG. 3. Diagrammatic drawing of stretched skin of *T. s. parietalis;* the scarlet markings extend farther dorsally than in *T. s. fitchi* and black spots are prominent on the ventrals laterally. Some individuals of *parietalis* have much paler ground color, resembling *ornata* except in minor details (× 2½).

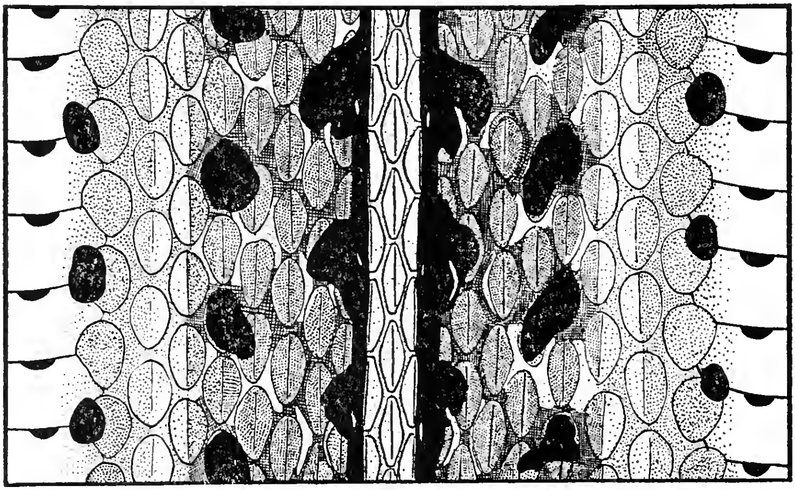

FIG. 4. Diagrammatic drawing of stretched skin of *T. s. ornata.* The ground color is like that of *parietalis* but paler with a continuous black area bordering the dorsal stripe (× 2½).

frequent variation was in heavy reddish suffusion on the sides of the head not found in typical *fitchi*. In each local population of this subspecies the characters seem to be remarkably uniform and stable.

T. s. parietalis differs from *fitchi* in several trenchant characters, and there are additional slight or average differences between the two. In approximate order of their importance the differences are as follows: 1) The red (or pale yellow or green or buffy) marks on skin between the scales on the upper half of the dorsolateral area (that is between the sixth and seventh, seventh and eighth and eighth and ninth scale rows) present in *parietalis* are missing in *fitchi* or are represented by only an occasional small fleck. 2) The dorsolateral area is black or nearly so in *fitchi* but averages paler in *parietalis,* in which a wide range of shades may be found from black to olive brown. 3) The red of the dorsolateral area frequently invades the lateral stripe, which sometimes is mostly red, and may even invade the ventrals in *parietalis,* but in *fitchi* the red marks are usually confined to the dorsolateral area, and do not invade the lateral stripe. 4) The prominent paired black dots or semicircular marks on the anterior edge of each ventral in *parietalis* are largely lacking in *fitchi,* which rarely has any dark marks on the ventral surface. 5) The dorsal stripe consistently involves the middorsal scale row and the adjacent half of the next row on each side, and is bright yellow in *fitchi,* but in *parietalis* it may be slightly wider, may be duller with more dusky suffusion, and its edges may be less sharply defined.

Intermediate and Atypical Populations

Of many specimens examined from eastern Oregon, Idaho, Utah, Wyoming and Colorado, few were typical of either *parietalis* or *fitchi.* Many were intermediate in some respects or showed a composite of characters of the two subspecies. No well-defined belt of intergradation exists, but the transition extends over more than a thousand miles, with local populations somewhat isolated and slightly differentiated along divergent lines. In view of this situation some plausibility could be claimed for any of several dividing lines between the subspecies. However, by far the most logical division is the Continental Divide; south of the Teton Range it constitutes a broad barrier separating eastern and western populations. Across Montana and Canada also it constitutes a more or less formidable barrier, with high altitudes and cold climates that probably are limiting to garter snakes. With few exceptions the snakes from east of the Continental Divide are more nearly like *parietalis* in the sum of their characters whereas those from west of the Divide are more nearly like *fitchi.*

In the Teton Range and in Yellowstone National Park these garter snakes occur in headwater streams up to the Continental Divide. KU 27956 from Two Ocean Lake 3½ miles northeast of Moran, Teton County, Wyoming, agrees in its characters with *fitchi,* having the red lateral marks small and inconspicuous, discernible only on the anterior half of the body. The dorsolateral area is dark, almost black. The ventrals lack dark markings.

In Utah, populations of *sirtalis* occur in the drainages of the Bear, Weber and Sevier rivers and other smaller streams of the western half of the state. Obviously the species invaded Utah from the north, probably at a time when Lake Bonneville, the predecessor of the present Great Salt Lake, drained into the Snake River of Idaho. Van Denburgh and Slevin (1918:190) separated from their western "*concinnus*" and "*infernalis*" and allocated to *parietalis* the populations of Utah and southeastern Idaho, but presumably these authors were not familiar with typical *parietalis* of the Mid-west. Subsequent authors (Wright and Wright, 1957:834; Stebbins, 1954: 505; Conant, 1958:328) have followed this arrangement. A re-examination of specimens from Utah, including living individuals collected at Bear Lake in the summer of 1959, indicates that they should be assigned to *fitchi* rather than to *parietalis.*

Likewise various specimens from the drainage basin of the Snake River in Idaho are predominantly *fitchi* in the sum of their characters, although they differ from that subspecies in its most typical form and resemble *parietalis* in some respects. KU 23133 from two miles east of Notus, Canyon County, Idaho, has the red crescents on the lower part of the sides (between scale rows six and seven) consistently developed on the anterior half of the body. KU 21873, a large female from Bannock County, Idaho, is exceptional in having small lateral black spots on the ventrals, resembling *parietalis* most closely in this respect. Also, it has the red lateral crescents unusually well developed; the first three series are conspicuous, those of the fourth series are consistently developed, and those of the fifth series show occasionally.

Forty-five specimens in the University of Colorado Museum from northwestern Colorado were subjected to pattern analysis. In three specimens the dorsolateral black area between the dorsal stripe and the lateral stripe on each side has no markings, and in eight others there is only an occasional fleck or crescent on the skin between the sixth and seventh scale rows. All others have the normal complement of dorsolateral crescents or flecks between the scales of rows three and four, four and five, and five and six. But, these specimens vary in extent of development of the crescents in the upper half of the dorsolateral area on each side—between scale rows six and seven, seven and eight, and eight and nine. Only six snakes show traces of the crescents of the uppermost series (between scale rows eight and nine). Development of these crescents is variable but in all the specimens the crescents are confined to the anterior half of the body. The crescents between rows six and seven and between seven and eight are present in 20 specimens and in ten of these the crescents are conspicuous and regularly arranged, often meeting and consequently form H-shaped markings. In most of the snakes the crescents are best developed in the second fifth of the body and disappear posteriorly. In five of the twenty, crescents between rows six and seven are fairly regular, but those between rows seven and eight are few and appear only sporadically. In eight specimens there are no crescents between either rows seven and eight or eight and nine. In eight others the crescents between rows six and seven are likewise absent, and only the crescents between rows three to six are present.

These specimens from Colorado also differ from typical *parietalis* in having the black spots on the anterolateral edges of the ventrals less developed. In three of the 45 these spots are lacking entirely and in four others they are few and small. In the majority of specimens the spots are from ¼ to ⅕ the length of the ventrals. In approximately one-third of the specimens the spots are absent posterior to mid-body. In five specimens obtained at Sheridan Lake, Pennington County, South Dakota, in the Black Hills in August, 1960, dorsolateral areas are dark with red crescents small and inconspicuous, and with black spots either lacking from the ventrals or only faintly developed. In two specimens from Sundance, Crook County, northeastern Wyoming, the red crescents are small and inconspicuous also. In one of these specimens, KU 28028, small black spots are present in the corners of the ventrals, but in the other, KU 23654, the spots are absent.

In having the dorsolateral area consistently black, with the three uppermost series of red crescents reduced or absent, and in having the ventral black spots reduced or absent, these specimens from Colorado, Wyoming, and South Dakota differ from more eastern and more typical *parietalis*, and tend toward *fitchi*, even more strongly than some Idaho specimens tend toward *parietalis*. Nevertheless, all things considered, the Continental Divide is the most logical boundary between the two subspecies, even though occasional individuals and even local populations deviate from the general trend of characters from east to west.

Acknowledgments

Dr. Doris M. Cochran of the United States National Museum kindly furnished information concerning the type specimen of *Eutainia dorsalis* formerly in the National Museum collection but now lost. Dr. James S. Findley of the University of New Mexico and Dr. Ralph J. Raitt of New Mexico State University contributed habitat notes and records of specimens and loaned us critical specimens of *T. sirtalis* from New Mexico. Drs. George F. Baxter of the University of Wyoming, John M. Legler of the University of Utah, and Wilmer W. Tanner of Brigham Young University kindly provided us with information concerning the specimens in the collections of their respective institutions, and their personal observations concerning the distribution of garter snakes in their states. Alice V. Fitch, Chester W. Fitch and Donald S. Fitch assisted in the collection of fresh specimens in Oregon and Utah and the unsuccessful search of many a mosquito-infested meadow in southern Wyoming and northwestern Colorado in July, 1959. Dr. R. G. Webb made available his MS on reptiles of Oklahoma.

This taxonomic study of garter snakes originated as a by-product of the senior author's study of ecology and economic bearing of snakes in the central Plains Region of the United States, for which support received from the National Science Foundation is gratefully acknowledged.

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(Contribution from The State Biological Survey, and from the Department of Zoology of The University of Kansas)

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Introduction

The Wakarusa River rises in the eastern edge of the Flint Hills and flows approximately 50 miles in an easterly direction and empties into the Kansas River near Eudora; with its tributaries, the Wakarusa drains 458 square miles in parts of Wabaunsee, Shawnee, Osage, and Douglas counties of northeastern Kansas (Fig. 1). The average gradient is 6.3 feet per mile. Turbidity is consistently more than 100 ppm in the lower portions of the mainstream and major tributaries, but is usually lower in the upper portions of tributaries. The channel of the mainstream is intrenched in its own alluvium (Dufford, 1958:36) and has high, muddy banks and mud- or sand-bottom; the upper parts of tributaries have lower banks and bottoms of gravel, rubble, or bedrock, although a few (such as Cole Creek) have areas of sandy bottom. A fringe forest of deciduous trees occurs along most streams. The topography and geology of the area have been discussed by Todd (1911), Franzen and Leonard (1943), and Dufford (1958).

The five-year period prior to 1957 was the driest in the 70-year history of weather-records in Kansas (Metzler *et al.*, 1958). Streams throughout the Wakarusa Basin suffered intermittency and, according to Mr. Melvon H. Wertzberger, the local Work Unit Conservationist with the Soil Conservation Service, many of them dried completely or contained only a few widely-scattered, stagnant pools. The effect of the drought on stream-flow at the mainstream gaging station 2.1 miles south of Lawrence is presented in Table 1.

According to the Division of Sanitation, Kansas State Board of Health, no untreated domestic sewage or industrial waste is discharged into the Wakarusa River System at this time.

The Wakarusa Watershed Association is in the preliminary stages of establishing a watershed control project in the basin. Objectives of the project are the improvement of land-use practices and the construction of several headwater retention structures. Such a program should have a long-range effect on the physical and biological characteristics of the streams of the basin. With this in

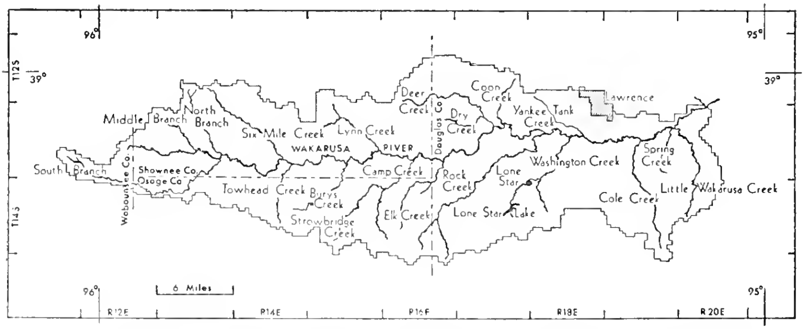

FIG. 1. Map of the Wakarusa River and its principal tributaries.

mind we think it important to document the nature of the present fish-fauna and to attempt a historical résumé of the fauna, based on collections made in the past sixty years.

Methods

Sodium cyanide, a 110-volt (600-watt) A. C. electric shocker, and seines (6, 12, and 25 feet long, 4 to 8 feet deep having ¼-in. mesh) were used to collect fish in 1959. All fishes were preserved and examined in the laboratory with the exception of large, common species that were identified in the field and returned to the stream.

TABLE 1. RECORD OF STREAM-FLOW, WAKARUSA RIVER 2.1 MI. S LAWRENCE, KANSAS.

WATER YEAR (Oct. 1 to Oct. 1)	Days with no flow	Days with flow less than 5 cfs	Maximum for year	Mean for year
1951	0	0	22,600	596.0
1952	0	85	5,000	179.0
1953	83	191	685	10.2
1954	194	123	2,010	17.2
1955	116	174	2,630	22.3
1956	122	183	2,550	20.7
1957	141	84	11,700	137.0
1958	0	9	6,370	213.0
1959	0	46	8,000	184.0

Collection Sites

The following collections were made by personnel of the State Biological Survey of Kansas in the 1890's, from 1910 to 1912, and from 1942 to 1953. These collections, all from Douglas County, are deposited in the Museum of Natural History, The University of Kansas. In the annotated list they are designated "KU":

1. Rock Creek, 1898.
2. Washington Creek, 1898.
3. "2½ miles east of Twin Mounds," Rock Creek, Sec. 1, T. 14 S, R. 17 E, 1899.
4. Rock Creek, 1911.
5. Rock Creek, 1912.
6. Washington Creek, 2¾ mi. W and 1 mi. S Lawrence, 1946.
7. Tributary of Yankee Tank Creek, Secs. 4 and 9, T. 13 S, R. 19 E, July 24, 1951.
8. Rock Creek, Sec. 19, T. 13 S, R. 19 E, Aug. 11, 1951.
9. Drainage ditch, tributary to Wakarusa River, Sec. 18, T. 13 S, R. 20 E, Aug. 24, 1951.
10. Wakarusa River, Sec. 20, T. 13 S, R. 20 E, Aug. 24, 1951.
11. Rock Creek, Sec. 27, T. 13 S, R. 18 E, Sept. 28, 1951.
12. Wakarusa River, Secs. 16 and 17, T. 13 S, R. 20 E, June 21, 1952.
13. Little Wakarusa River, Sec. 18, T. 13 S, R. 21 E, June 21, 1952.
14. Rock Creek, Sec. 33, T. 13 S, R. 18 E, Oct. 2, 1952.
15. Wakarusa River, Sec. 14, T. 13 S, R. 20 E, March 28, 1953.

Several collections made between 1912 and 1948 are deposited in the University of Michigan Museum of Zoology. In the annotated list these collections, all from Douglas County, are designated "UMMZ":

1. Rock Creek, June 9, 1912.
2. Oxbow Lake, 6 mi. E Lawrence, 1924 (several dates).
3. Wakarusa River, 7 mi. SE Lawrence, April 9, 1924.
4. Rock Creek, 9 mi. SW Lawrence, April 14, 1924.
5. Rock Creek, 12½ mi. S and 8½ mi. E Topeka, July 4, 1948.

Our collections, all of which were made in 1959, are identified by the letters DM followed by a station-number. Stations are numbered consecutively beginning at the mouth of the Wakarusa River and proceeding up each tributary as it is encountered.

Description of Stations

1. Wakarusa River, Sec. 4, T. 13 S, R. 21 E, March 14 and Oct. 18. Mouth of Wakarusa to one-half mile upstream; width *ca.* 25 feet; depth to 4 feet; bottom mud; banks mud, 10 feet high; current slight; water turbid.
2. Wakarusa River, Sec. 7, T. 13 S, R. 21 E, March 21. Width *ca.* 25 feet; bottom mud; banks mud, 10-20 feet high.
3. Little Wakarusa Creek, Sec. 19, T. 13 S, R. 21 E, May 2. Long sandy riffles, 6-10 inches deep; pools to 3 feet deep; bottom sand and mud; water slightly turbid.
4. Little Wakarusa Creek, Secs. 29 and 32, T. 13 S, R. 21 E, May 2. Riffles 8-10 inches deep having rubble bottom; pools to 4 feet deep having mud bottom; width 15-30 feet.
5. Little Wakarusa Creek, Sec. 7, T. 14 S, R. 21 E, May 2. Riffles 6-8 inches deep having gravel bottom; pools to 3 feet deep; bottom gravel and mud; width 8 to 15 feet; water slightly turbid.
6. Cole Creek, Sec. 21, T. 13 S, R. 20 E, May 2. Riffles 8-12 feet wide, 6 inches deep, bottom of flat, fragmented shale; pools having shale and mud bottom; water slightly turbid.
7. Cole Creek, Sec. 10, T. 14 S, R. 20 E, May 2. Small, shallow creek having sand bottom; water slightly turbid.

8. Cole Creek, Sec. 23, T. 14 S, R. 10 E, May 2. Banks steep, 20 feet high; bottom sand and hard clay; water clear.
9. Tributary to Yankee Tank Creek, Sec. 10, T. 13 S, R. 19 E, May 14. Width 2-10 feet; bottom mud; water turbid.
10. Washington Creek, Sec. 6, T. 14 S, R. 19 E, Feb. 26. Width *ca.* 25 feet; bottom rubble and gravel; water clear.
11. Washington Creek, Sec. 11, T. 14 S, R. 18 E, Feb. 26, March 28, March 30, and Oct. 18. One-half mile below dam at Lone Star Lake; width 10-15 feet; bottom gravel; water clear.
12. Tributary of east arm of Lone Star Lake, Sec. 13, T. 14 S, R. 18 E, March 31. Width 5-7 feet; bottom limestone rubble; water clear.
13. Tributary of southeast arm of Lone Star Lake, Sec. 24, T. 14 S, R. 18 E, March 30.
14. Tributary of southwest arm of Lone Star Lake, Sec. 22, T. 14 S, R. 18 E, March 30.
15. Tributary to Rock Creek, Sec. 34, T. 13 S, R. 18 E, Feb. 26. Width 10 feet; water clear.
16. Rock Creek, Sec. 7, T. 14 S, R. 18 E, July 25 and Oct. 18. Bottom gravel and mud; water clear.
17. Rock Creek, Sec. 23, T. 14 S, R. 17 E, July 25. Rubble riffles; pools having mud and sand bottom; water clear.
18. Wakarusa River, Sec. 14, T. 13 S, R. 18 E, July 23. Rubble riffles; pools having sand and mud bottom; water turbid.
19. Coon Creek, Sec. 27, T. 12 S, R. 18 E, March 21. Bottom rubble and mud; water clear.
20. Dry Creek, Sec. 8, T. 13 S, R. 18 E, May 16. Bottom rubble; water clear.
21. Deer Creek, Sec. 4, T. 13 S, R. 18 E, July. Pools having mud bottom; rubble riffles; water turbid.
22. Deer Creek, Sec. 31, T. 12 S, R. 18 E, March 21. Bottom mud and shale; water clear.
23. Elk Creek, Sec. 2, T. 14 S, R. 17 E, July 25. Stream intermittent; bottom rubble; water turbid.
24. Wakarusa River, ¼ mi. NE mouth of Elk Creek, Sec. 26, T. 14 S, R. 17 E, Oct. 17. Bottom mud and rubble; water turbid.
25. Camp Creek, Sec. 12, T. 14 S, R. 16 E, Oct. 17. Upland creek having clear, flowing water; rubble riffles alternating with shallow pools.
26. Strowbridge Creek, Sec. 11, T. 14 S, R. 16 E, July 25. Pools having bottom of mud and detritus, emitting malodorous gases; rubble riffles; water turbid.
27. Tributary of Strowbridge Creek, Sec. 29, T. 14 S, R. 16 E, July 30. Bottom rubble and mud; water clear, almost intermittent.
28. Lynn Creek, Sec. 24, T. 13 S, R. 16 E, April 4. Bottom rubble, mud and gravel; depth more than 6 feet; water turbid.
29. Lynn Creek, Sec. 14, T. 13 S, R. 16 E, May 27. Bottom mud and rubble; water turbid.
30. Lynn Creek, Secs. 14 and 15, T. 13 S, R. 16 E, July 28. Pools having sand bottom; rubble riffles; water clear.
31. Lynn Creek, Sec. 10, T. 13 S, R. 16 E, July 28. Bottom sand, rubble and mud; water clear.
32. Tributary to Lynn Creek, Secs. 11 and 12, T. 13 S, R. 16 E, May 16. Bottom rubble; water clear.
33. Burys Creek, Sec. 8, T. 14 S, R. 16 E, July 25. Bottom mud, rubble and detritus; rubble riffles; water turbid.
34. Wakarusa River, Sec. 28, T. 13 S, R. 16 E, July 28. Bottom mud and rubble; rubble riffles; water turbid.

35. Unnamed tributary of Wakarusa River, Sec. 24, T. 13 S, R. 15 E, April 4. Bottom mud; water turbid.
36. Six Mile Creek, Sec. 17, T. 13 S, R. 15 E, May 16. Bottom gravel and rubble; rubble riffles; water clear.
37. Wakarusa River, Sec. 25, T. 13 S, R. 14 E, May 16. Bottom mud and coarse sand; water turbid.
38. South Branch of Wakarusa River, Sec. 8, T. 14 S, R. 14 E, July 30. Bottom rubble and gravel; water clear.
39. South Branch of Wakarusa River, Sec. 5, T. 14 S, R. 13 E, July 30. Bottom bedrock; flow slight; rubble riffles; water turbid.
40. South Branch of Wakarusa River, Sec. 36, T. 13 S, R. 12 E, July 30. bottom mud; rubble riffles; water turbid.
41. Middle Branch of Wakarusa River, Sec. 21, T. 13 S, R. 14 E, April 4. Bottom mud; gravel riffles; water turbid.
42. Tributary of Middle Branch of Wakarusa River, Sec. 29, T. 13 S, R. 14 E, April 4. Bottom mud and bedrock; rubble riffles; water turbid.

Annotated List of Species

Lepisosteus osseus oxyurus Rafinesque. DM 2. The longnose gar is abundant in most large rivers of Kansas. The scarcity in the Wakarusa is probably attributable to the small size of the stream.

Lepisosteus platostomus Rafinesque. UMMZ 2. The shortnose gar is common in the Kansas River but seems less inclined than the longnose gar to ascend small streams.

Dorosoma cepedianum (LeSueur). UMMZ 2; DM 1. Gizzard shad.

Carpiodes velifer (Rafinesque). UMMZ 2. This record for the highfin carpsucker is based on a single specimen (UMMZ 63182). It was re-examined by Bernard Nelson who stated (personal communication) "The dorsal fin is broken and the 'pea-lip' smashed. A trace of the 'pea' is still discernible. The body is deeply compressed and other measurements agree with [those of] *C. velifer*. It was identified as *C. cyprinus* at first, but later changed by Hubbs." *C. velifer* probably was more abundant in Kansas during and before the early 1900's than at present. Several early records of the species are available, but the only specimen obtained in Kansas in recent years was captured in the Neosho River by Deacon in 1958.

Moore (1957:80) states that *C. velifer* occurs in the clearer rivers and lakes of the Mississippi valley, westward to Nebraska and Oklahoma. The almost complete disappearance of this species from Kansas probably resulted from an increase in turbidity, of the rivers, accompanying settlement and cultivation of the land.

Carpiodes carpio carpio (Rafinesque). KU 5, 12, 15; DM 1, 16, 21, 37. The river carpsucker occurred at stations scattered throughout the drainage, except in the smallest creeks. The largest numbers were found in the lower mainstream.

Ictiobus cyprinella (Valenciennes). KU 10; UMMZ 2; DM 1. The bigmouth buffalo was taken only near the mouth of the river; black buffalo, *Ictiobus niger* (Rafinesque) and smallmouth buffalo, *Ictiobus bubalus* (Rafinesque), possibly also occur there but were not taken in our survey.

Catostomus commersonnii commersonnii (Lacépède). KU 4, 8, 14; UMMZ 1, 5; DM 10, 11, 15, 16, 21, 23, 25, 26, 27, 29, 34, 42. The white sucker occurs primarily in upstream-habitats in the Wakarusa Basin.

Moxostoma aureolum (LeSueur). KU 15; DM 1. The northern redhorse was taken only in downstream portions of the basin. Minckley and Cross (1960) regard specimens from the Wakarusa River as intergrades between *M. a. aureolum* and *M. a. pisolabrum.*

Cyprinus carpio Linnaeus. KU 9, 12, 15; DM 1, 2. The carp, though most abundant in downstream situations, probably occurs throughout the drainage and is a potential pest in all impoundments likely to be constructed in the basin.

Notemigonus crysoleucas (Mitchill). KU 9; DM 9, 27, 33, 41. The golden shiner was found only in tributaries.

Semotilus atromaculatus (Mitchill). KU 2, 3, 5, 6, 7, 8, 10, 12, 13, 14; UMMZ 4, 5; DM 3, 9, 10, 11, 15, 16, 17, 18, 19, 20, 21, 23, 24, 25, 26, 29, 30, 31, 32, 33. The creek chub was usually abundant in small upland tributaries.

Hybopsis biguttata (Kirtland). KU 1, 3; UMMZ 4. The hornyhead chub seemingly was common in early collections but has not been found since 1924. The fish characteristically inhabits clear streams having gravel-bottom. Disappearance of the species from the Wakarusa may have resulted from increased siltation and intermittency of flow.

Hybopsis storeriana (Kirtland). KU 10; UMMZ 3.

Hybopsis aestivalis (Girard). KU 10; UMMZ 3; DM 1. This species and the preceding one are common in the Kansas River but do not ascend far up the Wakarusa. *Hybopsis gelida* (Girard) and *Hybopsis gracilis* (Richardson) occur in the Kansas River and may be expected in the lowermost portion of the mainstream of the Wakarusa.

Notropis percobromus (Cope). KU 12; DM 1, 2. The plains shiner shows little tendency to move far upstream from the Kansas River, where it is abundant.

Notropis umbratilis (Girard). KU 5, 11, 14; UMMZ 1, 4, 5; DM 9, 10, 11, 16, 17, 18, 21, 22, 23, 24, 25, 26, 29, 32, 33, 34, 35, 37, 38, 39, 41. In our survey the redfin shiner was the most abundant species at several stations, especially at those in the lower and middle portions of tributaries to the mainstream.

Notropis cornutus frontalis (Agassiz). KU 1, 2, 3, 8, 11, 14; DM 16. Judging from the numbers preserved in early collections, the common shiner was more abundant and widespread in the 1890's than in 1959. A watershed improvement program effecting more stable flow and decreased turbidity might benefit this shiner.

Notropis lutrensis (Baird and Girard). KU 1, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15; UMMZ 1, 2, 3, 4, 5; DM all stations *except* 5, 11, 12, 13, 14, 19, 35. The red shiner was ubiquitous, and was the dominant species at a majority of stations.

Notropis stramineus (Cope). KU 7, 8, 10, 11, 12, 13, 14, 15; DM 1, 2, 3, 4, 6, 7, 9, 10, 15, 16, 17, 24, 25, 31, 37. The sand shiner was most common in two environments: (1) near the mouth of the Wakarusa where abundance of the species may be attributed to the close proximity of a large population of *N. stramineus* in the Kansas River, and (2) in upland tributaries that drain areas in which sand is found (especially in Cole Creek).

Notropis topeka (Gilbert). KU 1, 14; UMMZ 1, 4, 5; DM 22, 25, 27, 33. Minckley and Cross (1959) describe the habitat of the Topeka shiner as pools of clear upland tributaries with slight flow. We found the Topeka shiner in such habitat in Deer Creek, Strowbridge Creek and Burys Creek. The largest population occurred in a tributary of Strowbridge Creek. This stream probably was intermittent in 1958, and Deer and Burys creeks may have been intermittent at some time in 1957-1959. Although Minckley and Cross (1959:215) have stated that Rock Creek is "unsuitable for this species," we suspect that Rock Creek served as a refugium for *N. topeka* in time of drought. It was found there (KU 14) in 1952, and again (DM 16) on April 8, 1960.

Notropis buchanani Meek. UMMZ 3. Inclusion of the ghost shiner is based on two specimens (UMMZ 63107) collected by C. W. Creaser in 1924.

Phenacobius mirabilis (Girard). KU 6, 7, 8, 10, 11, 12, 13, 15; UMMZ 4; DM 3, 6, 16, 18, 21, 22, 34. The suckermouth minnow occurred in several collections but was nowhere dominant. The largest populations were at DM 3, 6, and 22.

Hybognathus nuchalis Agassiz. KU 8, 15; UMMZ 3; DM 1, 6. The silvery minnow was taken only in the downstream portion of the Wakarusa and its lower tributaries.

Pimephales promelas Rafinesque. KU 6, 7, 8, 9, 10, 11, 13, 14, 15; UMMZ 1, 4, 5; DM all stations *except* 1, 8, 10, 11, 13, 14, 30. The fathead minnow was ubiquitous, and was dominant at several stations on the smallest creeks.

Pimephales notatus (Rafinesque). KU 1, 6, 11, 12, 14, 15; UMMZ 1, 4, 5; DM 6, 8, 10, 12, 16, 17, 18, 24, 25, 26, 37, 41. The bluntnose minnow occurred at several stations on tributaries but was not common.

Campostoma anomalum (Rafinesque). KU 7, 8, 10, 11, 12, 13, 14; UMMZ 4, 5; DM 3, 9, 10, 11, 13, 15, 16, 17, 18, 19, 20, 21, 22, 24, 25, 30, 32, 33, 34. The stoneroller was usually abundant at upstream stations and was found in the mainstream of the Wakarusa River.

Ictalurus punctatus (Rafinesque). KU 6, 8, 10, 11, 12, 13, 15; DM 1, 2, 18, 24. Channel catfish were taken by us only in the mainstream; anglers sometimes catch channel catfish in several of the tributaries.

Ictalurus melas (Rafinesque). Black bullhead. KU 1, 2, 5, 6, 9, 14; UMMZ 2, 5; DM 5, 6, 7, 16, 17, 21, 25, 26, 31, 32, 33, 38, 39, 40.

Ictalurus natalis (LeSueur). Yellow bullhead. KU 9, 14.

Pylodictis olivaris (Rafinesque). KU 8, 10; DM 18. The flathead catfish comprises a small but consistent part of the sport fishery of the Wakarusa, especially in the mainstream.

Noturus flavus Rafinesque. Stonecat. KU 10, 11, 12.

Noturus exilis (Nelson). DM 11. The slender madtom is recorded only from riffles in Washington Creek below Lone Star Lake. These riffles, because of the influence of the reservoir, are probably the most permanent in the drainage at present. The slender madtom may become more widespread if other reservoirs are built that stabilize stream flow in the basin.

Perca flavescens (Mitchill). The yellow perch is present in Lone Star Lake, and probably will become established in future reservoirs that are constructed.

Percina caprodes (Rafinesque). Log perch. KU 11, 14, 15; DM 11, 12, 16, 37, 41.

Etheostoma nigrum Rafinesque. KU 8, 14; UMMZ 1, 3, 4, 5; DM 16, 17. The johnny darter, like the common shiner, has been taken recently only in Rock Creek, where darters flourish. Often, ten to fifteen johnny darters were taken with one sweep of a 6- or 12-foot seine in shallow pools having mud bottoms. Watershed improvement may benefit this species.

Etheostoma spectabile pulchellum (Girard). KU 7, 10, 12, 14; UMMZ 4, 5; DM 10, 11, 12, 13, 14, 16, 17, 21, 22, 23, 24, 26. The orangethroat darter was most abundant in Deer Creek, Rock Creek and Washington Creek.

Micropterus salmoides salmoides (Lacépède). DM 16, 17, 21, 30, 32, 34, 37. The largemouth bass occurs throughout the drainage at present, and should become established without supplemental stocking in future reservoirs. The absence of this species in early collections suggests that widespread stocking of bass in various impoundments in the area in recent years has increased populations in the streams. An anomalous individual, lacking a right pelvic fin, was found in Lone Star Lake.

Chaenobryttus gulosus (Cuvier). The warmouth is present in Lone Star Lake. This species typically inhabits lakes and probably will establish itself in other reservoirs.

Lepomis cyanellus Rafinesque. Green sunfish. KU 6, 8, 9, 10, 11, 13, 14, 15; UMMZ 2, 4, 5; DM all stations *except* 11, 12, 13, 14, 27, 30, 31, 39, 40.

Lepomis macrochirus Rafinesque. KU 6; DM 10, 16, 17, 24, 31, 33, 37, 41, 42. Both bluegill and green sunfish are common throughout the drainage and will contribute to the sport fishery of any reservoir constructed. The absence of the bluegill in early collections suggests that its population has increased recently owing to introductions in many impoundments.

Lepomis humilis (Girard). Orangespotted sunfish. KU 6, 9, 11, 14, 15; UMMZ 1, 2, 4, 5; DM 4, 6, 16, 17, 21, 23, 24, 25, 26, 32, 33, 34, 37, 38, 39, 40, 41, 42.

Lepomis megalotis breviceps (Rafinesque). Longear sunfish. KU 8 (one individual taken in Rock Creek, 1951).

Pomoxis annularis (Rafinesque). KU 9, 15; UMMZ 2. White crappie occur in Lone Star Lake and in farm ponds in the basin.

Pomoxis nigromaculatus (LeSueur). Specimens of black crappie were obtained from Lone Star Lake and in farm ponds in the basin.

Aplodinotus grunniens Rafinesque. Drum. KU 12.

Discussion

Our data show that the present fish-fauna of the Wakarusa River has three major components:

(1) A group of species that are mainly restricted to the lower mainstream; all of them are common in the Kansas River (*Lepisosteus osseus, Carpiodes carpio carpio, Ictiobus cyprinella, Moxostoma aureolum, Cyprinus carpio, Hybopsis storeriana, Hybopsis*

aestivalis, Notropis percobromus, Hybognathus nuchalis and *Pylodictis olivaris*).

(2) A group of species that are ubiquitous; they comprised the entire fauna in some tributaries, despite the existence of habitats that seemed suitable for other species (*Notropis lutrensis, Pimephales promelas, Ictalurus melas,* and *Lepomis cyanellus*).

(3) A group of species having distributions centered in Rock Creek, Washington Creek, Deer Creek, and some nearby tributaries (*Catostomus commersonnii, Semotilus atromaculatus, Hybopsis biguttata, Notropis cornutus, Notropis topeka, Notropis umbratilis, Phenacobius mirabilis, Pimephales notatus, Campostoma anomalum, Noturus exilis, Percina caprodes, Etheostoma nigrum* and *Etheostoma spectabile*).

The distributions of groups (2) and (3) provide clues to the effect of drought on the fish-population, and on the relative ability of various species to repopulate areas where they have been extirpated.

Larimore *et al.* (1959) studied the re-establishment of stream-fish following drought in Smiths Branch, a small warmwater stream in Illinois. They found that 21 of the 29 species regularly occurring there reinvaded most of the stream-course within two weeks after the resumption of normal flow, and that all but three species were present by the end of the first summer. Our study indicates a much slower rate of dispersal by many of the same species. This is presumably attributable to the ecological barrier presented by the Wakarusa mainstream.

During the drought (1952-1956) the mainstream with its turbid water and mud bottom could hardly have served as a refugium for species requiring the clear water and gravel bottom of upland tributaries. Probably the main refugia for these species [group (3)] were in the upper portions of Rock Creek, Washington Creek and possibly Deer Creek. While collecting we observed that these creeks had larger proportions of gravel-rubble bottom, clearer water, deeper pools, and appeared to be more stable than other creeks in the drainage. In Washington Creek, Lone Star Lake enhanced stability of flow.

At the end of the drought, fishes in group (3) probably were extirpated or decimated in other tributaries of the Wakarusa. After normal flow recommenced in 1956, fishes re-entered the previously uninhabitable streams or stream-segments. The rate of redispersal by various species probably depended upon their innate mobility, and upon their tolerance of the muddy mainstream of the Wakarusa.

Our observations suggest that certain species in group (3) dispersed rapidly from refugia in Rock Creek, Washington Creek, and possibly Deer Creek. These species may, of course, have survived in a few remaining pools in tributaries throughout the basin, thereby necessitating only minor redispersal within these tributaries following drought.

Species of group (3) that were most tolerant of drought or that dispersed most rapidly are *Catostomus commersonnii*, *Notropis umbratilis*, *Pimephales notatus*, and *Percina caprodes;* these were present in the uppermost portions of the basin in 1959. Fishes having lesser capacity for survival or dispersal are *Semotilus atromaculatus*, *Notropis topeka*, *Phenacobius mirabilis* and *Campostoma anomalum;* in 1959, they were not found farther upstream than Burys Creek. *Etheostoma spectabile*, the orangethroat darter, was taken in Rock Creek, Washington Creek, Deer Creek, Strowbridge Creek, Elk Creek, and at station 24 on the Wakarusa. This is a riffle-dwelling, comparatively sedentary fish, not a strong swimmer. These traits, coupled with the long, muddy pools and infrequent riffles of the Wakarusa mainstream, provide a reasonable explanation of the comparatively slow rate of dispersal by the orangethroat darter.

Several species showed no tendency for redispersal following drought, in that they were confined to Washington Creek or Rock Creek in 1959. *Noturus exilis* was taken only in Washington Creek immediately below Lone Star Lake. Rock Creek is the last stream in the Wakarusa Basin in which *Notropis cornutus*, *Hybopsis biguttata* and *Etheostoma nigrum* have survived. These species require comparatively permanent streams having pool-and-riffle habitats and gravelly bottoms for spawning. *Hybopsis biguttata* has been recorded only from Rock Creek, where it was last taken in 1924. It is interesting to note that this species had not reinvaded Smiths Branch, in Illinois, three years after the resumption of stream-flow (Larimore *et al.*, 1959). *Notropis cornutus* and *Etheostoma nigrum*, although formerly more widespread in the Wakarusa Basin, have been taken recently only in Rock Creek.

Faunal changes that have occurred in the basin in the past 60 years indicate a decrease in extent of clear, continuously flowing stream-habitat.

Comparisons with Faunas of Nearby Streams

Minckley (1959) reported 13 species from the Big Blue River Basin that were not taken in our survey of the Wakarusa. Most of the 13 are fishes that probably occur throughout the lower mainstream of the Kansas River and might enter the lower Wakarusa occasionally. *Chrosomus erythrogaster* and *Notropis rubellus* were reported by Minckley but have not been found in the Kansas River Basin east of the Flint Hills, either in recent or in early collections. On the other hand, five species have been reported from the Wakarusa but not from the Big Blue River. Two of these, *Notemigonus crysoleucas* and *Chaenobryttus gulosus*, may have been introduced by man. The remaining three, *Hybopsis biguttata, Noturus exilis* and *Percina caprodes,* have not been taken farther west than Mill Creek, Wabaunsee County. In general the faunas of the two systems are similar; forty species are common to both.

Comparison of the faunal list reported from the Cottonwood River drainage (Arkansas River System) by Cross (1954) with that here reported reveals 26 species in common, 19 found only in the Wakarusa and 15 species found only in the Cottonwood.

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CONTENTS

INTRODUCTION

The flathead chub, *Hybopsis gracilis* (Richardson), occurs in the Plains Region of Canada and the United States, in four major drainage systems: Mackenzie River, which discharges into the Arctic Ocean; Saskatchewan River, which discharges into Hudson Bay via Nelson River; and Missouri-Mississippi System and Rio Grande, both draining into the Gulf of Mexico. Each of these systems is occupied in part only. In the Mackenzie Basin, *H. gracilis* has been reported as far north as Fort Good Hope (Walters, 1955:347). Flathead chubs occur in the Saskatchewan Basin from Alberta eastward to Lake Winnipeg, Manitoba, but have not been found in other streams that flow into Lake Winnipeg (Red River, Brokenhead River and Whitemouth River) nor in Nelson River downstream from Lake Winnipeg. In the Missouri Basin the species occurs more or less continuously from the high plains adjacent to the Rocky Mountains in Montana and Wyoming down the mainstream of the Missouri River to its mouth, and down the mainstream of the Mississippi River as far as Barfield, Arkansas, but not to the Gulf. The species probably attains its greatest abundance in the Missouri Basin, but it is scarce or absent in tributaries north and east of the Missouri mainstream, in the South Platte Basin, and in the central part of the Platte River in Nebraska. The flathead chub is unknown in the Mississippi Basin above the mouth of the Missouri River, and in the Ohio River Basin above its mouth. In the Arkansas River Basin, records are restricted to (1) the headwaters and tributaries of the Arkansas River from eastern Colorado downstream as far as Garden City, Kansas, (2) the Cimarron River at Kenton, Cimarron County, Oklahoma, and (3) the South Canadian River and tributaries from northeastern New Mexico eastward as far as Norman, McClain County, Oklahoma, but rarely there. Thus, the range in the Arkansas Basin seems to consist of three isolated segments. Likewise, isolated populations exist in the Rio Grande System, where flathead chubs are confined to the upper parts of the Rio Grande and Pecos basins, above the confluence of the Rio Grande and Pecos Rivers. Records resulting from introductions have been reported for the Gila River by Koster (1957:62) and from the Snake River, Wyoming, by Simon (1946:72).

Six names apply to the flathead chub, the earliest of which is *Cyprinus gracilis* Richardson (1836:120). Other names have sometimes been accepted as applicable to valid species and/or subspecies, but usage, diagnoses, and stated ranges have been confusingly inconsistent. For most of the past 100 years, *Platygobio* Gill has been recognized as the appropriate generic name for the flathead chub, but Bailey (1951:192) places *Platygobio* and other nominal genera of barbeled minnows having short guts, protractile premaxillae, and four teeth (primary row) in the single genus *Hybopsis* (Agassiz, 1854). Strangely, the orthotype of *Hybopsis, H. gracilis* Agassiz, is a junior synonym of *H. amblops* (Rafinesque) (Hubbs and Ortenburger, 1929b:66) and is a younger name than *C. gracilis* Richardson.

The purpose of this paper is to redescribe the species and to make known its pattern of geographic variation. Natural history will also be considered, as will habitat, food habits, and breeding season.

METHODS, MATERIALS AND ACKNOWLEDGMENTS

Ten meristic characters and seventeen measurements of body-parts (the latter expressed as proportions of standard length) have been analyzed. They are: number of rays in the dorsal, anal, caudal, pectoral and pelvic fins; number of scales in the lateral line, before the dorsal fin, around the body and around the caudal peduncle; number of vertebrae; body-depth, depth of caudal peduncle, length of caudal peduncle, predorsal length, length of depressed anal and dorsal fins, length of pectoral and pelvic fins, head-length, head-depth, head-width, snout-length, postorbital length of head, length of orbit, interorbital width, length of upper jaw and width of gape.

Counts and measurements were made as described by Hubbs and Lagler (1958), with the exception of scales before the dorsal fin, which were counted as the number of vertical scale-rows between the upper margin of the opercular cleft and the origin of the dorsal fin. Vertebral counts, made from roentgenograms, excluded vertebrae in the Weberian complex (presumably always four) but included the hypural vertebra.

Counts and measurements were made on series (usually ten fish) from localities throughout the range. To minimize effects of allometric growth, the fish were divided into several length-groups prior to analysis of proportional measurements: 30-50mm, 50-70mm, 70-100mm, 100-150mm, 150-200mm and 200mm standard length and over. The majority of specimens examined were 70-100mm in standard length.

Specimens were obtained from the following institutions: University of Alberta (abbreviated AU in the text); Museum of Zoology, University of Michigan (UMMZ); University of Missouri (UM); Montana State College (MSC); University of Oklahoma Museum of Zoology (UOMZ); University of Saskatchewan; Royal Ontario Museum, Division of Zoology, Toronto (ROMZ); University of Wyoming (WU); Museum of Natural History, University of Kansas (KU). Specimens examined are listed in the accounts of the subspecies.

We are grateful to D. A. Boag, Reeve M. Bailey, Arthur L. Witt, C. J. D. Brown, Carl Riggs, F. M. Atton, W. B. Scott, and George Baxter, all staff-members of the institutions listed in the immediately preceding paragraph, for placing specimens at our disposal. Mr. William Peters analyzed the contents of stomachs of specimens that were used for study of the food habits. Mr. Artie L. Metcalf assisted in collecting specimens. Drs. Kenneth B. Armitage and E. Raymond Hall offered valued suggestions in connection with the preparation of the manuscript.

DESCRIPTION OF THE SPECIES

Hybopsis gracilis (Richardson)

Flathead Chub

(Synonymy under accounts of subspecies)

Description.—Pharyngeal teeth 2,4-4,2, hooked; dorsal fin of moderate size, falcate, first principal ray longest, extending beyond posterior rays in depressed fin, its origin usually slightly in front of insertion of pelvic fin, approximately equidistant from tip of snout and base of caudal fin, rays 8, rarely 9; pectoral fin strongly falcate, rays 14-20, usually 16-18; pelvic rays 8, rarely 9; anal fin falcate, rays 8, rarely 9; caudal rays 19, rarely 20.

Body slightly compressed, nearly terete; head-length 23.1-28.8 per cent of standard length; head broad and flattened, snout subconical, premaxillae protractile, upper lip not medially expanded; mouth subterminal, nearly horizontal, large; a single pair of terminal maxillary barbels; orbit usually 5-7 per cent of standard length; lateral line slightly decurved; intestine short, peritoneum silvery.

Color brown or olivaceous dorsally, silver or creamy white ventrally, without distinctive markings; dusky lateral band evident in preserved specimens.

Taste-buds present on membrane between first and second principal rays of all fins, and on first to sixth interradial membranes of pectoral fin. On the caudal fin, taste buds between first and second principal rays of upper and lower lobes, though present, are less well developed than on other fins. Moore (1950:88) states that taste buds are numerous on the barbels, cheeks, lips, chin, snout, opercles and branchial membranes, and are present in decreasing numbers over the body.

Nuptial tubercles of male minute and densely scattered over top of head and snout; usually present on pectoral rays 1-8, weak when present on rays beyond the eighth, never found beyond the eleventh ray; minute tubercles usually found on dorsal, pelvic and anal fins, rarely on lower scales of caudal peduncle; predorsal scales have a fine peripheral row of tubercles.

Hybopsis gracilis gracilis (Richardson)

(Plate 22)

Cyprinus (Leuciscus) gracilis Richardson, 1836:120 and Pl. 78 (original description; Saskatchewan R. at Carlton House).

Coregonus angusticeps Cuvier and Valenciennes, 1848:534 (original description; Saskatchewan R.).

Pogonichthys communis Girard, 1856:188 (in part; original description); Girard, 1858:247 and plate 55 (in part; characters; synonymy); Suckley, 1860:361 (Milk R.); Cope, 1879:440 (Fort Benton, Mo. R.; Judith R.).

Platygobio gracilis, Jordan and Gilbert, 1882:219 (in part; characters; synonymy); Graham, 1885:74 (Kansas R.; synonymy); Jordan, 1885:29 (records); Jordan and Meek, 1886:13 (Mo. R., St. Joseph, Mo.); Meek, 1892:245 (characters; Mo. R., Sioux City, Iowa); Eigenmann, 1895:111 (Craig; Poplar; Brandon; Medicine Hat); Meek, 1895:137 (Platte R., Fremont, Neb.); Evermann and Cox, 1896:412 (in part; habitat; synonymy); Jordan and Evermann, 1896:326 (in part; characters; synonymy); Thompson, 1898:214 (Brandon; Saskatchewan R.); Evermann and Goldsborough, 1907:98 (records from Canada); Forbes and Richardson, 1920:170 (characters; habitat; synonymy; records from Illinois; but Fig. 45 is *Hybopsis meeki* Jordan and Evermann, not *H. gracilis*); Hankinson, 1929:446 (records from North Dakota); Jordan, 1929:76 (in part; characters); Jordan, Evermann and Clark, 1930:136 (in part; synonymy); Churchill and Over, 1933:45 (characters; food; habitat; spawning; records from South Dakota); O'Donnel, 1935:481 (Ohio R., Cairo, Ill.; Miss. R., Chester, Ill.); Hinks, 1943:57 (records from Canada); Clemens, *et al.*, 1947:17 (records from Saskatchewan); Dymond, 1947:19 (distribution in Canada); Rawson, 1951:208 (Great Slave Lake; Mackenzie R.); Shoemaker, Pickering and Durham, 1951:84 Miss. R., Cates, Tenn.; Miss. R., between Hickman and Barfield, Ark.); Wynne-Edwards, 1952:18 (distribution in Canada); Miller and Paetz, 1953:47 (Peace R. at town of Peace River); Walters, 1955:347 (distribution in Canada; dispersal into Canada); Keleher, 1956:265 (Saskatchewan R., Manitoba); Lindsey, 1956:771 (distribution in Canada); Keleher and Kooyman, 1957:110 (Kelsey Lake, Manitoba); Lindsey, 1957:657 (Laird and Peace drainages, British Columbia); Scott, 1958:16 (distribution in Canada); Slastenenko, 1958:7 (distribution in Canada).

Platygobio pallidus Jordan and Gilbert, 1882:220 (original description; Ohio R., Cairo, Ill.); Jordan and Evermann, 1896:326 (characters; synonymy; Ohio R., Cairo, Ill.); Jordan, Evermann and Clark, 1930:136 (Ohio R., Cairo, Ill.; synonymy).

Platygobio gracilis communis, Simon, 1946:71 (in part; characters; food; habitat; spawning); Moore, 1950:87 (habitat; sense organs).

Hybopsis gracilis communis, Bailey, 1951:192 (record from Iowa; key); Harlan and Speaker, 1951:75 (characters; distribution in Iowa); Hubbs, 1951:9 (habitat; Miss. R.); Harrison and Speaker, 1954:516 (habitat); Personius and Eddy, 1955:42 (habitat; Little Mo. R.).

Hybopsis gracilis, Cleary, 1956:271 (record from Iowa; distributional map); Bailey, 1956:332 (record from Iowa; key); Harlan and Speaker, 1956:90 (characters; distribution in Iowa); Eddy, 1957:111 (in part; characters; key); Moore, 1957:110 (in part; key); Underhill, 1959:100 (Vermillion R., South Dakota).

Diagnosis.—Post-Weberian vertebrae 40-42, usually 41-42; lateral line scales 50-56; pectoral rays 15-20, usually 17 or more; head-depth 12.3-15.1 per cent of standard length, usually 14.7 per cent or less. See Figs. 1 and 2.

Other characters.—Circumference scale-rows 31-42; predorsal scale-rows 20-29; size large, as much as 246 mm standard length (see Fig. 1 of Pl. 24); head-length 23.4-27.4 per cent of standard length, usually 25.5 per cent or less; post-orbital length of head 10.9-13.9 per cent of standard length, usually 12.5 per cent or less; predorsal length 46.0-51.7 per cent of standard length; orbit 5.1-6.8 per cent of standard length; prepelvic length 46.6-52.2 per cent of standard length; caudal peduncle length 17.2-22.1 per cent of standard length.

Range (Plate 21).—Mackenzie Basin south from Fort Good Hope; Saskatchewan Basin east to Lake Winnipeg; mainstream of Missouri River and Mississippi River south to Barfield, Arkansas; intergrading with *H. g. gulonella* in upper Missouri Basin and lower parts of major tributaries to Missouri River in Nebraska and Kansas.

Specimens examined.—Below are listed museum numbers, number of specimens (in parentheses), localities, and year of collection. Collections marked with asterisk (*) are intergrades more closely resembling *H. g. gracilis* than *H. g. gulonella*. Records from literature are cited in the synonymy.

ALBERTA: UA (6), Milk R. at town of Milk River, 1950; UA (3), Athabasca R. at Fort McMurray, 1955; UA (1), Red Deer R. at Steveville, 1952; UA (2), Peace R. at town of Peace River, 1952; UA (11), Peace R. at Dunvegan, 1956; UA (2), Simonette R. tributary to Smoky R., date unknown; ROMZ 17704 (1), Milk R. W town of Milk River, 1955.

ARKANSAS: UMMZ 128573 (5), Mississippi Co., Mississippi R., 1939.

ILLINOIS: UMMZ 134799 (146), Mississippi R. at Grand Tower, 1936; UMMZ 147045 (8), Mississippi R. at Cairo, 1944.

KANSAS: KU 1234 (173), Leavenworth Co., backwater of Missouri R. near Corral Cr., 1940; * KU 1814 (1), Douglas Co., floodpool of Kansas R., below Lakeview, 1951; * KU 1825 (1), Douglas Co., floodpool of Kansas R., 1951; * KU 1841 (56), Douglas Co., Kansas R. at Lawrence, 1951; * KU 1898 (6), Douglas Co., floodpool of Kansas R., 1951; * KU 1911 (5), Douglas Co., floodpool of Kansas R., 1951; * KU 1928 (2), Jefferson Co., floodpool of Kansas R., 1951; KU 3850 (30), Atchison Co., Missouri R., 1957; * KU 4377 (2), Douglas Co., Kansas R. at Lawrence, 1958; * KU 4655 (2), Douglas Co., Kansas R. at Lawrence, 1959.

MANITOBA: ROMZ 13834 (1), Kelsey Lake, 25 miles east of the Pas, no date; ROMZ 14500 (25), Saskatchewan R. at the Pas, 1947; ROMZ 16325 (1), Lake Winnipeg, no date.

MISSOURI: UMMZ 147126 (130), Mississippi R. at Cliff Cave, 1944.

MONTANA: * MSC 1878 (36), Carbon Co., Elbow Cr., 1957; * MSC 1943 (11), Phillips Co., Frenchman Cr., 1957; * MSC 2021 (10), Pondora Co., Marias R., 1955; * MSC 2022 (4), Lewis and Clark Co., Missouri R. below Holter

Dam, 1948; * MSC 2052 (6), Gallatin Co., Missouri R. near Trident, 1948; * MSC 3074 (3), Custer Co., Hardy Reservoir, 1952; UMMZ 94146 (34), near mouth of Powder R., 1926.

NEBRASKA: * KU 4158 (9), Holt Co., Niobrara R. 6 mi. N Midway, 1958; * UM (field no. 59-81) (56), Butler Co.-Colfax Co. line, Platte R. 1.5 mi. S Schuyler, 1959; * UM (field no. 59-74) (5), Dodge Co., Platte R. 1 mi. S North Bend, 1959; UMMZ 134826 (46), Otoe Co., Missouri R. 1.5 mi. E Minersville, 1940; UMMZ 134799 (67), Cass Co., Missouri R., 1940; UMMZ 135341 (43), Knox Co., Missouri R. 2 mi. NE Niobrara, 1940; UMMZ 135818 (95), Thurston Co., Missouri R. NE Macy, 1941.

NORTHWEST TERRITORY: ROMZ 13627 (1), Great Slave Lake, no date; ROMZ 13628 (1), Great Slave Lake, no date.

SASKATCHEWAN: * ROMZ 3885 (2), Sucker Cr., trib. Cypress Lake, 1927; ROMZ 14368 (2), South Saskatchewan R. at Yorath Island, 1941; ROMZ 16620 (5), South Saskatchewan R. at Saskatoon, 1953; KU 5126 (5), South Saskatchewan R. at Birson Ferry, 1957; KU 5127 (3), South Saskatchewan R. at Leader, 1957; KU 5128 (2), North Saskatchewan R. at Cecil Ferry, 1957; KU 5129 (1), South Saskatchewan R. at Clarkboro Ferry, 1957.

SOUTH DAKOTA: * KU 4961 (9), Haakon Co., Bad R. at Midland, 1959; * KU 4963 (17), Washabaugh Co., White R. 6 mi. SW Belvidere, 1959; * UMMZ 120362 (168), White R. 6.5 mi. S Kadoka, 1934; * UMMZ 127484 (11), Todd Co., Little White R., 1934; UMMZ 127488 (29), Charles Mix Co., Missouri R., 1934; * UMMZ 127678 (32), Cheyenne R., E Wasta, 1939; UMMZ 166762 (21), Hughes Co., Missouri R. 3 mi. NE Pierre, 1952; * UMMZ 166803 (91), Harding Co., Little Missouri R. at Camp Crook, 1952; UMMZ 166845 (121), Carson Co.-Walworth Co. line, Missouri R. 2.5 mi. N Mobridge, 1952; UMMZ 166985 (61), Yankton Co., Missouri R. at Yankton, 1952.

WYOMING: * WU 2073 (6), Washakie Co., Big Horn R. at Worland, 1956.

Hybopsis gracilis gulonella (Cope)

(Plate 23)

Pogonichthys communis Girard, 1856:188 (in part; original description); Girard, 1858:247 (in part; characters; synonymy); Cope and Yarrow, 1875:653 (characters; Pueblo, Colo.).

Pogonichthys (Platygobio) gulonellus Cope, 1864:277 (original description; near Bridger's Pass, Wyo.).

Platygobio gulonellus Cope, 1865:85 ("Platte R., near Fort Riley" [Fort Riley is on Kansas R., not Platte R.; Cope's specimens probably are from Platte drainage, on basis of known distributions of other species reported]).

Ceratichthys physignathus Cope and Yarrow, 1875:651 (original description; Arkansas R., Pueblo, Colo.).

Platygobio communis, Gill, 1876:408 (characters; Platte Valley; Green River, Utah [the latter probably erroneous]).

Couesius physignathus, Jordan and Gilbert, 1882:219 (characters; synonymy; Arkansas R., Pueblo, Colo.); Jordan, 1885:29 (records).

Platygobio gracilis, Jordan and Gilbert, 1882:219 (in part; characters; synonymy); Cragin, 1885:109 (Garden City, Kans.); Gilbert, 1885:98 (Garden City, Kans.); Jordan, 1885:29 (records); Evermann and Cox, 1896:412 (in part; habitat; synonymy); Jordan and Evermann, 1896:326 (in part; characters; synonymy); Ortenburger and Hubbs, 1927:125 (Canadian R., Norman, Okla.); Hubbs, 1927:75 (parasites; teratology; records from New Mexico); Hubbs and Ortenburger, 1929a:28 (S. Canadian R., Durham, Okla.); Jordan, 1929:76 (in part; characters); Jordan, Evermann and Clark, 1930:136 (in part; synonymy).

Platygobio physignathus, Jordan and Evermann, 1896:325 (characters; synonymy; records from upper Arkansas R.); Ellis, 1914:62 (characters; synonymy; records from Colorado); Cockerell, 1927:123 (distribution in Colorado); Jordan, Evermann and Clark, 1930:136 (synonymy; records from upper Arkansas R.).

Platygobio gracilis communis, Simon, 1946:71 (in part; characters; food; habitat; spawning).

Platygobio gracilis gulonellus, Simon, 1946:72 (characters; records from Wyoming; Arkansas R.).

Platygobio gracilis: communis × *gulonellus,* Simon, 1946:92 (North Platte R., Neb.-Wyo. line).

Platygobio gracilis physignathus, Moore, 1950:87 (habitat; sense organs).

Hybopsis gracilis communis, Beckman, 1952:50 (characters; food; habitat); Cross, Dalquest and Lewis, 1955:222 (records from Texas).

Hybopsis gracilis physignathus, Beckman, 1952:50 (characters; habitat).

Hybopsis gracilis, Eddy, 1957:111 (in part; characters; key); Koster, 1957:61 (characters; habitat; spawning; food); Moore, 1957:110 (in part; key); Smith, 1958:177 (fossil record; Doby Springs, Okla.).

Diagnosis.—Post-Weberian vertebrae 36-38, rarely 39; lateral line scales 42-54, usually less than 50; pectoral rays 14-19, usually fewer than 17; head-depth 13.5-18.0 per cent of standard length, usually 14.8 per cent or more. See Figures 1 and 2.

Other characters.—Circumference scale-rows 30-40, slightly fewer than in *H. g. gracilis;* predorsal scale-rows 17-27, somewhat fewer than in specimens from Canada, but much the same as specimens from the Missouri-Mississippi system; size small, rarely as much as 130 mm standard length (Fig. 1 of Pl. 24); head-length 24.0-28.0 per cent of standard length, usually more than 25.5 per cent; postorbital length of head 11.2-14.4 per cent of standard length, usually more than 12.5 per cent (both characters illustrate the larger head of *H. g. gulonella);* predorsal length 46.4-52.7 per cent of standard length, longer than in the other subspecies; orbit 5.0-6.6 per cent of standard length; prepelvic length 47.4-53.7 per cent of standard length, longer than in *H. g. gracilis;* caudal peduncle length 17.1-22.7 per cent of standard length, essentially the same in both subspecies.

The label on types of this subspecies, in the Academy of Natural Sciences of Philadelphia, states merely "near Bridger's Pass, Wyo., Expedition of 1856, Dr. W. A. Hammond" (letter from Dr. James Böhlke to Cross, dated Jan. 27, 1960). Dr. Hammond was a surgeon who also collected scientific specimens, assigned to an expedition under the command of Lt. F. T. Bryant. Bryant's log is recorded in the Proceedings of the 35th Congress (1858:455-481). The site at which these specimens were taken cannot be ascertained from the log, but study of it is helpful in indicating the probable locations.

The expedition left Fort Riley on June 21, 1856, on the following route: up Republican River; across to Fort Kearney on Platte River; west along Platte River to S. Platte River; up S. Platte River to Pole (Lodgepole) Creek; Pine Bluffs (Neb.-Wyo. line); across East Fork to West Fork of Laramie River; Cooper's Creek; West Fork of Medicine Bow; Pass Creek and down canyon of Pass Creek; across N. Platte River; up Sage Creek; on August 15, camped on Muddy Creek, tributary to Green River (first record of fish, trout); back to Sage Creek; August 19-21, camped on island in North Platte River; to Pass

Creek; Elk Creek; west branch of Medicine Bow; Aspen Creek; West Fork of Laramie River; August 29, to East Laramie River where a large supply of fish was caught; tributary of Cache la Poudre then downstream to mouth of this river; down South Platte River past mouth of Crow Creek and Beaver Creek; left South Platte River 14 miles below mouth of Beaver Creek, toward Republican River; down Rock Creek to Arikaree; down Arikaree to Republican River and down the Republican to Fort Riley.

Mention is made of fish only twice in the entire log. We doubt that Muddy Creek or the East Laramie River is the type locality of *P. gulonellus,* because the flathead chub has not since been found in either of these streams. The most likely collection site for *P. gulonellus* is the North Platte River near the mouth of Sage Creek, in what is now Carbon County, Wyoming, where the expedition was camped for three days. This species is known to occur in the North Platte River, and since the type locality is reported as "near Bridger's Pass" this is the probable location.

Range (Plate 21).—Upper mainstream and tributaries of Rio Grande, Pecos, Arkansas and North Platte Rivers; isolated populations in tributaries of the upper Missouri River.

Specimens examined.—Below are listed museum numbers, number of specimens (in parentheses), localities and year of collection. Series marked by asterisks (*) are intergrades tending toward *H. g. gulonella.* Literature reports are cited in the synonymy.

COLORADO: KU 4742 (162), Bent Co., Purgatoire R. at Las Animas, 1959; KU 4748 (105), Pueblo Co., Arkansas R. at west edge of Pueblo, 1959; KU 4758 (50), Fremont Co., Arkansas R. at Florence, 1959; KU 4769 (64), Fremont Co., Beaver Cr., 1959.

KANSAS: KU 2648 (2), Finney Co., Arkansas R., 1958; KU 2858 (13), Finney Co., Arkansas R. at Garden City, 1951; KU 3964 (12), Kearney Co., Arkansas R., 1958; * KU 4041 (2), Cheyenne Co., Republican R., 1958; KU 4732 (30), Hamilton Co., Arkansas R. at Kendall, 1959; * KU 4868 (1), Kansas-Nebraska line, Republican R. 1.5 mi. S. Hardy, 1959.

MONTANA: * MSC 1960 (8), Powder River Co., E. Fork of Powder R., 1957; MSC 2010 (64), Dawson Co., Redwater R., 1957.

NEBRASKA: * KU 2140 (2), Dawson Co., Platte R., at Gothenburg, 1931; * KU 4863 (20), Furnas Co., Republican R. at Cambridge, 1959; * UM (field no. 59-49) (74), Scotts Bluff Co., North Platte R. at Morrill, 1959; * UMMZ 133918 (17), Dixon Co., Logan Cr., 1939; * UMMZ 134813 (31), North Platte R., Neb.-Wyo. line, 1941; * UMMZ 135084 (14), Harlan Co., Beaver Cr. 0.25 mi. S Stamford, 1940; * UMMZ 135200 (41), Scotts Bluff Co., North Platte R. 1 mi. SE Henry, 1940; * UMMZ 135280 (59), Cherry Co., Niobrara R. 3 mi. SE Valentine, 1940; * UMMZ 135700 (25), Buffalo Co., South Loup R. 8 mi. N Miller, 1941; * UMMZ 135778 (54), Thurston Co., Logan Cr. 2.5 mi. W Pender, 1941; * UMMZ 135786 (25), Dixon Co., Logan Cr. 0.5 mi. NW Wakefield, 1941.

NEW MEXICO: KU 4219 (50), Colfax Co., Cimarron Cr. at Springer, 1958; KU 4235 (19), Mora Co., Sapello Cr. near Sapello, 1958; KU 4245 (157), Bernalillo Co., Rio Grande 12 mi. S Bernalillo, 1958; KU 4255 (22), Rio Arriba Co., Rio Grande at Velarde, 1958; KU 4266 (53), Sandoval Co., Rio Grande 2 mi. N Cochiti Pueblo, Marcelino Baca bridge, 1958; KU 4269 (91), San Miguel Co., Pecos R., 3 mi. S Pecos, 1958; KU 4274 (25), Sandoval Co., Jemez R. at Jemez Canyon Dam, 1958; KU 4294 (113), Guadalupe Co., Pecos R. 3 mi. N Dilia, 1958; UMMZ 94897 (146), Pecos R. at San Juan, 1926; UMMZ 94898 (1), Pecos R. at San Juan, 1926; UMMZ 118209 (68), Sapello

Cr. at Sapello, 1937; UMMZ 133131 (7), Pecos R. 0.5 mi. N Santa Rosa, 1940; UMMZ 133136 (1), Rio Grande at Albuquerque, 1940.

OKLAHOMA: KU 2329 (1), Cleveland Co.-McClain Co. line, S. Canadian R., 1952; UOMZ 26355 (10), Cimarron Co., Cimarron R. 2 mi. N. Kenton, 1957; UOMZ 5917 (2), Cleveland Co., S. Canadian R. S Norman, 1925.

TEXAS: KU 3409 (18), Hemphill Co., Canadian R. at town of Canadian, 1955.

WYOMING: WU 2084 (4), Platte Co., N. Platte R. at Glendo, 1956; WU 2095 (3), Converse Co., N. Platte R. at Douglas, 1956; UMMZ 104064 (58), N. Platte R. below Guernsey Dam, 1937; * UMMZ 114642 (7), drainage ditch in Wind R. drainage, 1936; * UMMZ 114644 (20), drainage ditch at Riverton, 1936; * UMMZ 127518 (63), Weston Co., Beaver Cr., 1934; * UMMZ 127681 (20), Big Horn Co., Big Horn R. tributary, 1939; * UMMZ 136488 (9), Crook Co., Belle Fourche R. 15 mi. N Devil's Tower, 1941; * WU 2122 and two uncatalogued series at WU (13), Belle Fourche R., no precise locality or date; UMMZ 159969 (14), Natrona Co., N. Platte R. 2 mi. E Casper, 1950.

INTRASPECIFIC VARIATION

Two subspecies of *H. gracilis* are recognized by us: one northern and eastern, characteristically inhabiting large rivers (*H. g. gracilis*), and one southern and western, characteristically inhabiting small streams (*H. g. gulonella*). Other scientific names that have been applied to this fish in the past are listed in the synonymy.

H. g. gulonella is a chubby, deep-bodied fish, whereas *H. g. gracilis* is long and slender. The head of the creek subspecies is deeper and longer than that of *H. g. gracilis*, being rounded anteriorly when seen in sideview. The head of the large-river subspecies is acutely wedge-shaped in profile. *H. g. gracilis* has a larger orbit than *H. g. gulonella*. Fins of *H. g. gracilis* are more strongly falcate than those of the other subspecies. *H. g. gracilis* has a greater number of lateral line scales, pectoral rays and post-Weberian vertebrae than the creek subspecies. The large-river subspecies attains much larger size than does the creek subspecies (Plate 24). Except in areas of intergradation, complete separation of the two subspecies can be made on the basis of lateral line scales, pectoral rays, post-Weberian vertebrae and head-depth. The regressions of head-depth on standard length in *H. g. gracilis* from the Saskatchewan River (several localities) and in *H. g. gulonella* from Beaver Creek, Arkansas River Drainage (KU 4769) are shown in Plate 24. Although values for the largest specimens of *H. g. gracilis* are omitted from Plate 24, the regression remains essentially linear to standard lengths of approximately 250 mm. On the basis of head-depth alone, separation of the two subspecies is possible in specimens larger than 40 mm. Similar results were obtained by using the regression of postorbital length on standard length, and could have been obtained by using other proportional measurements.

NATURAL HISTORY

Habitat

The species inhabits alkaline streams with shifting sand bottoms where the waterlevel fluctuates considerably with heavy rains and melting snow. The flathead chub is found in silty water and often is the predominant species in streams that have high turbidity. The remarkable ability of this fish to withstand exceedingly high turbidity is illustrated by its predominance in the Little Missouri River, which has an average concentration of suspended silt two and one-half times that of the Missouri River at Kansas City (Personius and Eddy, 1955:42).

H. g. gracilis is found in large rivers throughout its range, occa-

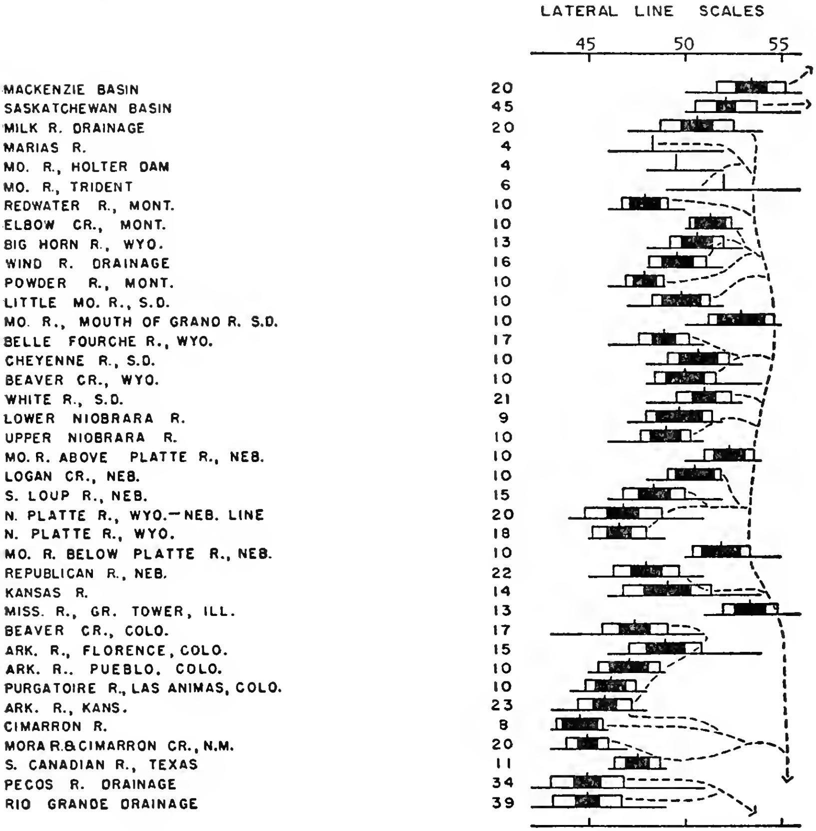
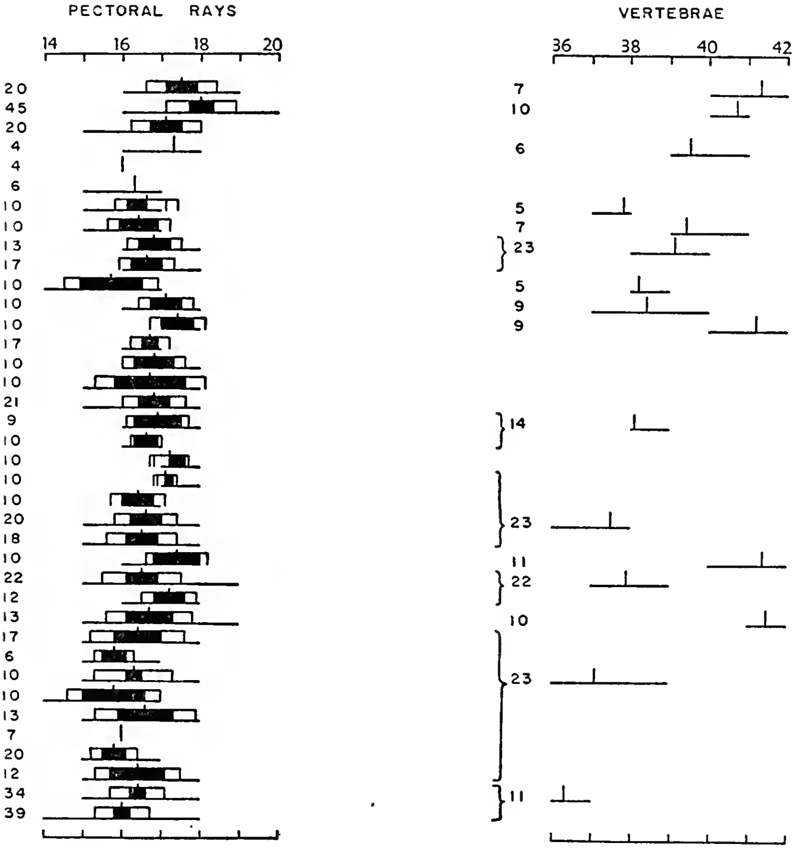


Figure 1. Graphic analysis of lateral line scales, pectoral rays and post-Weberian vertebrae in *Hybopsis gracilis*. In each symbol, horizontal line = range, vertical line = mean, open rectangle = one standard deviation on each side of mean, black rectangle = twice the standard error on each side of mean.

sionally migrating into smaller streams, especially in the spawning season. It prefers the main channel of rivers in moderate to strong current. All series examined are from elevations lower than 3,000 feet.

H. g. gulonella occupies small rivers and creeks, preferring pools with moderate currents. In fall, dense concentrations of this subspecies have been found in small pools, where brush, driftwood or other debris deflects the current and prevents filling with drifting sand. Hundreds of flathead chubs were collected in such pools in the Purgatoire and Arkansas rivers. Specimens were also collected with ease in Beaver Creek, Colorado, from pools with murky water and slight flow, over bottoms of gravel and bedrock. No brush or



Numbers to left of symbols = number of specimens examined from that locality; combined collections indicated by brackets. The dash-lines represent drainage patterns of rivers in which this species occurs.

other debris was near the pools. In each case the streams carried little water, although they undoubtedly carry greater volumes of water in spring and early summer after rains and spring thaws. The preferred bottom-type for this subspecies seems to be gently shifting sand.

H. g. gulonella is found in warm-water streams, whereas *H. g. gracilis* occurs in cooler water. The southwestern subspecies was taken in August in the Mora River drainage at Sapello (temperatures above 80° F.) but not at Mora (temperatures below 70° F.). In the Purgatoire River, a thriving population was found where the water temperature was 92° F., on September 6, 1959. In the Arkansas and Pecos rivers and the Rio Grande this subspecies is most abundant below the mountainous parts of the stream-courses, but at elevations higher than 4,000 feet on the plains.

Associated Species

In the Pecos and Arkansas basins, species commonly taken with *H. g. gulonella* are *Catostomus commersonnii, Hybognathus placita,*

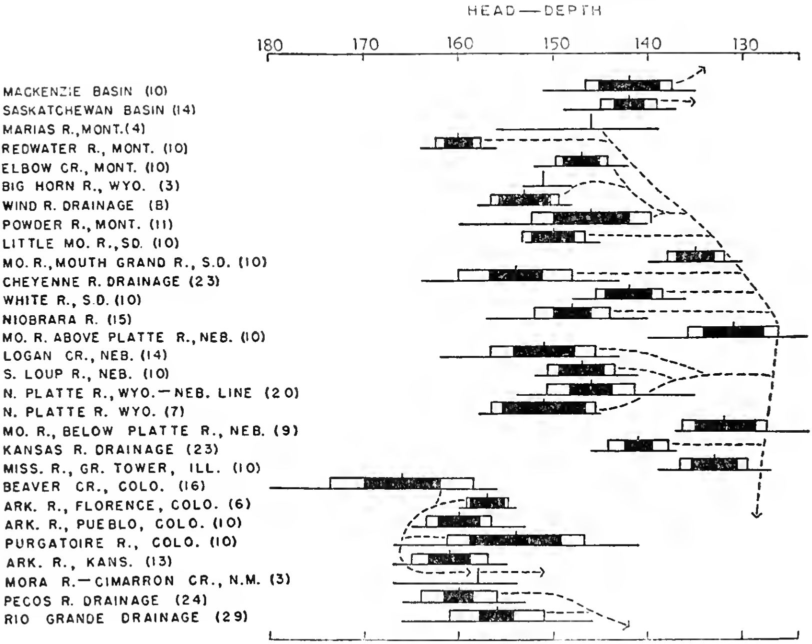
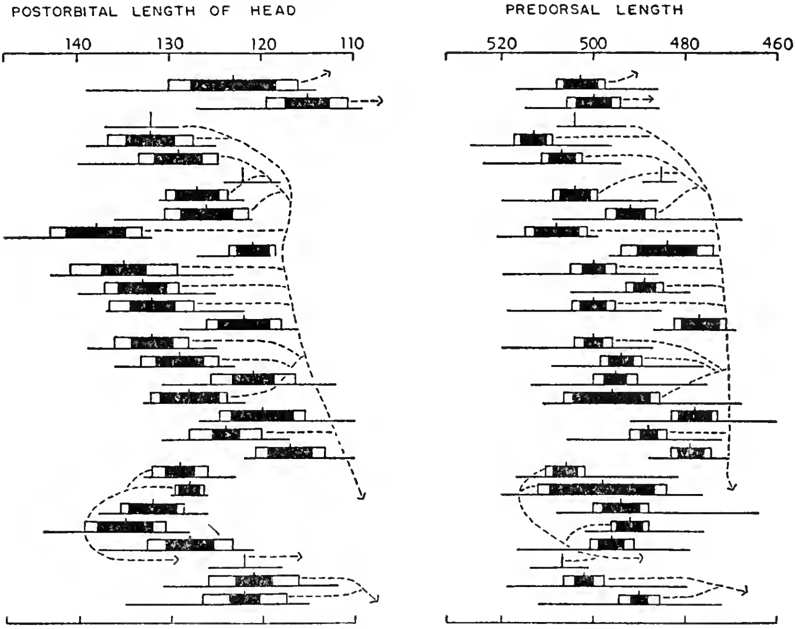


FIGURE 2. Graphic analysis of head-depth, postorbital length of head and predorsal length of *Hybopsis gracilis,* expressed as thousandths of standard length. Numbers in parenthesis = number of specimens examined from each locality. In each symbol, horizontal line = range, vertical line = mean, open

Notropis lutrensis lutrensis, Notropis stramineus missuriensis, Pimephales promelas, and *Campostoma anomalum plumbeum.* The only spiny-rayed fishes that we have found with *H. g. gulonella* are *Lepomis cyanellus* and *L. humilis,* both of which are scarce. Associates of *H. g. gracilis* include the same species, plus other ostariophysan fishes such as species of *Carpiodes, Ictiobus,* and silt-adapted species of *Hybopsis* and *Notropis.*

We failed to find the flathead chub at any of 11 localities in the South Platte drainage, where we collected in September, 1959. Dr. George Baxter, of the Department of Zoology, University of Wyoming, told us that he has never found *H. gracilis* in that drainage. The fauna of the South Platte includes *Catostomus catostomus, Semotilus atromaculatus, Hybopsis biguttata, Hybognathus hankinsoni, Notropis cornutus frontalis, Etheostoma nigrum* and *E. exile*—species rarely if ever found with *H. gracilis.*

Ecologically, *H. g. gulonella* seems to be the counterpart of *Semotilus atromaculatus* in streams where the latter species is absent. Observations of *H. g. gulonella* in the Purgatoire River indicated



rectangle = one standard deviation on each side of mean, black rectangle = twice the standard error on each side of mean. The dash-lines represent drainage patterns of rivers in which this species occurs. All measurements are of specimens 70 to 100 mm in standard length.

that loosely-organized groups of flathead chubs congregated one to four inches above the bottom of pools, and near or under protective cover such as roots of vegetation or debris lodged against shore. Individuals moved about independently within the group (rather than as schools), and occasionally rose to the surface, perhaps for food.

Food

The flathead chub is chiefly carnivorous, but its food includes some aquatic vegetation (Table 1). Most organisms found in specimens (both subspecies) were terrestrial insects (Coleoptera, Diptera, Orthoptera); all insects were adult stages, except those designated as larvae in Table 1. Roundworms probably were parasites, rather than food.

Hubbs (1927:76) states that the food of young flathead chubs that were obtained from the Arkansas River System in New Mexico consisted "almost entirely of crustaceans (small ostracods and cladocerans to the exclusion of all else but an occasional larval or adult insect, etc.)."

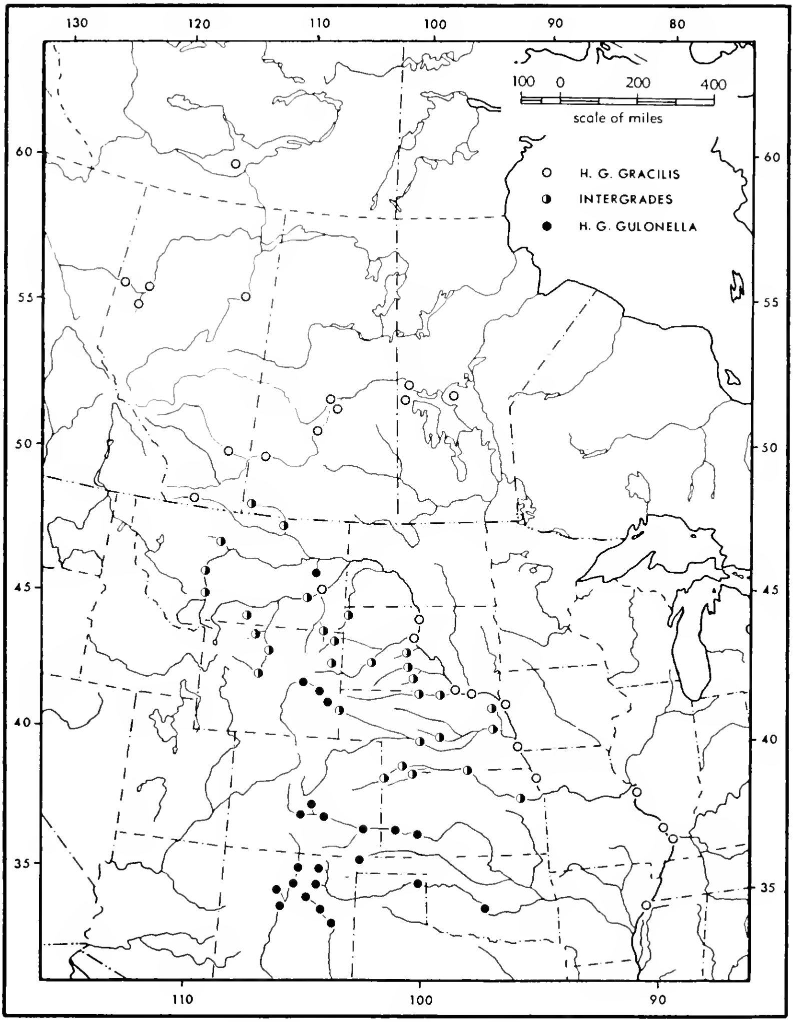
Spawning Season

Specimens of *H. g. gulonella* that have been examined reach sexual maturity at approximately 65 mm standard length. Most specimens of *H. g. gracilis* less than 85 mm in standard length are immature, but larger specimens probably are mature.

The spawning season is in late summer, beginning in July and extending into September. Specimens from the Peace River, collected on August 10, 1952, include females that were mostly spent and tuberculate males. Males and females in spawning condition were collected in the Milk River in August of 1955. A large prespawning female was obtained in Red Deer River in June of 1952. A male from Fort McMurray had fairly well developed tubercles on August 9, 1955. A prespawning female was taken from the Saskatchewan River at Clarkboro Ferry on June 7, 1957. Tuberculate males were collected in the Powder River on June 30, 1957. Specimens from the White River in South Dakota, collected on July 7, 1934, include tuberculate males. The specimens discussed above are *H. g. gracilis* or intergrades tending toward that subspecies.

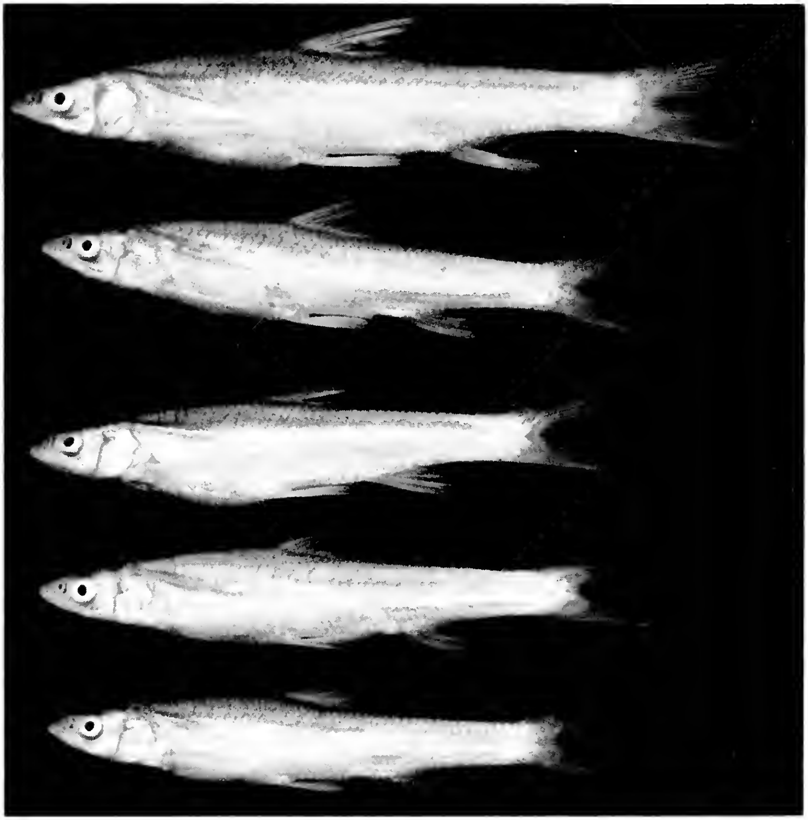
Specimens of *H. g. gulonella* collected in the Arkansas River at Pueblo and Florence, Colorado, on September 7, 1959, include some tuberculate males, although most females are spent. On August 8, 1957, a series of flathead chubs that includes tuberculate males was collected in the Redwater River, Montana. In the Pecos River on

PLATE 21



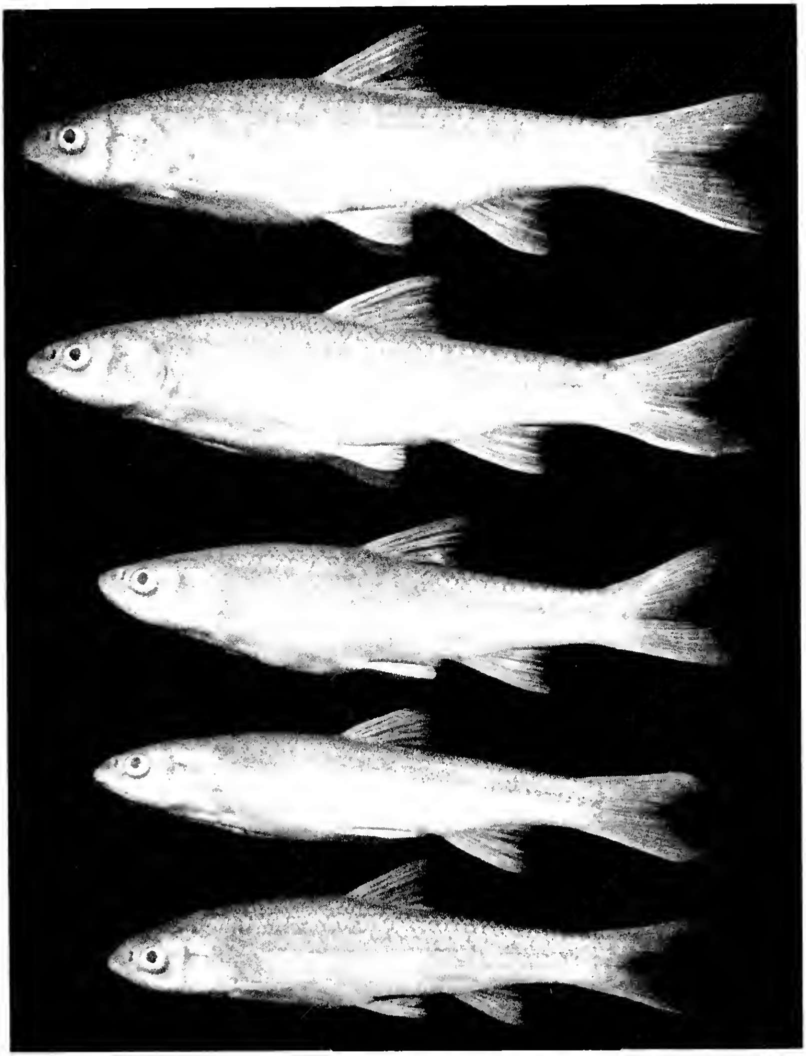
Distribution of collections examined.

PLATE 22



Hybopsis gracilis gracilis. Missouri River, Thurston County, northeast of Macy, Nebraska. Largest specimen 87.5 mm standard length.

PLATE 23



Hybopsis gracilis gulonella. Pecos River, San Miguel County, 3 miles south of town of Pecos, New Mexico. Largest specimen 91 mm standard length.

PLATE 24

FIG. 1. Top: *Hybopsis gracilis gracilis,* 230.0 mm standard length, one of the largest specimens examined. Missouri River, Carson County-Walworth County line, 3 miles northeast of Mobridge, South Dakota, at mouth of Grand River.

Bottom: *Hybopsis gracilis gulonella,* 121.6 mm standard length, the largest specimen examined of this subspecies. Beaver Creek, Fremont County, 10 miles northeast of Florence, Colorado, on Highway 115.

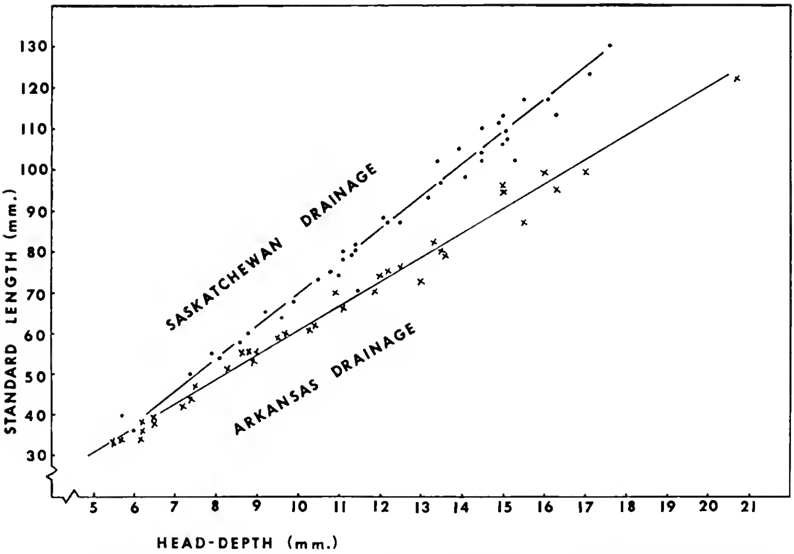


FIG. 2. Regression of head-depth on standard length in *Hybopsis gracilis gracilis* from the Saskatchewan River, and in *H. g. gulonella* from Beaver Creek, Arkansas River Drainage (KU 4769).

TABLE 1. ORGANISMS FOUND IN STOMACHS OF HYBOPSIS GRACILIS FROM VARIOUS LOCATIONS, EXPRESSED AS PERCENTAGE OF TOTAL VOLUME.

	S. Saskatchewan R., Clarkboro Ferry, Sask.	Milk R., Alberta	Missouri R., S. D.	Missouri R., Neb.	Arkansas R., Fremont Co., Colo.	Arkansas R., Pueblo Co., Colo.	Pecos R., San Miguel Co., N. M.
No. specimens examined....	1	7	6	10	10	10	10
No. specimens containing food..................	1	6	1	2	1	3	7
KIND OF ORGANISM							
Aphasmidia...............	10.0	00.7	......	03.0	......	......	......
Arthropoda							
Araneae							
Argiopidae.........	......	......	......	......	04.0	......	......
Theridiidae.........	......	......	......	......	04.0	......	......
Insecta							
Ephemeroptera (nymph)							
Baetidae........	......	05.0	......	......	......	......	......
Heptagenidae....	......	08.0	......	......	......	......	......
Hemiptera							
Corixidae........	35.0	00.3	......	......	......	......	......
Hymenoptera							
Formicidae......	......	21.0	......	......	......	......	60.0
Coleoptera							
Staphylinidae....	......	01.7	07.0	......	......	......	......
Scolytidae.......	......	13.3	70.0	......	......	......	......
Tenebrionidae....	......	05.7	......	......	70.0	......	......
Carabidae.......	......	05.7	......	......	......	01.0	......
Curculionidae....	......	01.0	......	......	......	......	......
Coccinellidae.....	......	......	......	......	......	......	09.0
Trichoptera (case)...	......	01.7	......	......	......	......	......
Diptera							
Mymaridae......	......	00.3	......	......	......	......	......
Empididae.......	......	01.3	......	......	......	......	......
Cecidomyiidae....	......	......	......	......	04.0	......	......
Trachinidae......	......	00.7	......	......	......	......	......
Simulidae.......	......	06.7	20.0	......	......	......	......
Tabanidae.......	......	......	......	......	06.0	......	......
Chironomidae....	......	......	......	......	06.0	......	......
Not identified to family.......	......	01.0	......	......	......	......	......
Orthoptera							
Locustidae.......	......	07.7	......	......	......	......	......
Tettigoniidae.....	......	......	03.0	70.0	......	......	09.0
Tetrigidae.......	......	......	......	......	06.0	......	......
Homoptera							
Fulgoridae.......	......	05.0	......	......	......	......	01.0
Insect egg..........	......	00.7	......	......	......	......	......

TABLE 1. ORGANISMS FOUND IN STOMACHS OF HYBOPSIS GRACILIS FROM VARIOUS LOCATIONS, EXPRESSED AS PERCENTAGE OF TOTAL VOLUME.—*Concluded*

	S. Saskatchewan R., Clarkboro Ferry, Sask.	Milk R., Alberta	Missouri R., S. D.	Missouri R., Neb.	Arkansas R., Fremont Co., Colo.	Arkansas R., Pueblo Co., Colo.	Pecos R., San Miguel Co., N. M.
Plants							
Cyanophyceae	......	09.0	......	......	......	99.0	20.0
Cyperaceae	......	02.0	......	......	......	......	01.0
Zannichellia palustris	......	00.3	......	......	......	......	......
Vascular remains	55.0	......	......	27.0	......	......	......
Miscellaneous							
Sand	......	00.7	......	......	......	......	......
Pharyngeal tooth	......	00.3	......	......	......	......	......
Total (%)	100.0	99.8	100.0	100.0	100.0	100.0	100.0

August 25, 1958, spawning seemingly had been completed, although a few males still bore tubercles.

Spawning apparently occurs when river levels recede to the seasonal lows. In late summer, temperatures of these rivers probably are maximal, their turbidities are reduced, and their sandy bottoms are stable. Underhill (1959) reports that this species is rare in the Vermillion River, a northeastern tributary of the Missouri River, except in autumn when large numbers occur near the mouth of the river. We suspect that this is associated with spawning.

DISCUSSION

Hybopsis gracilis is highly variable in several morphological characteristics, including size and shape of head, body, and fins, and number of scales, vertebrae, and fin-rays. The variations are correlated in a way that indicates the existence of two subspecies. One of these, *H. g. gracilis,* attains large size, and has 1) a slender, streamlined body, 2) a depressed head that is acutely wedge-shaped in profile, 3) strongly falcate fins with the dorsal and pelvic fins originating anteriorly, and 4) many scales, vertebrae, and pectoral fin-rays. The second subspecies, for which *H. g. gulonella* is the oldest applicable name, is small, and has 1) a deep, chubby body, 2) head convex in dorsal contour (less depressed than in *H. g. gracilis*), 3) fins less falcate than in the latter subspecies, with the dorsal and pelvic fins originating more posteriorly, and 4) fewer scales, vertebrae, and pectoral fin-rays than *H. g. gracilis.* These differences are consistently expressed throughout the size-ranges of the subspecies, and in series collected at the same or nearby localities in several different years. Considerable variability was found in features other than those mentioned above, but individual variation among specimens from the same locality and adjacent localities is so great that none is diagnostic of subspecies. For example, orbital size and length of fins (but not their falcate shape) are variables that have little diagnostic value, although both features seem to vary in clinal fashion, with the higher values in the north.

Variation in *H. gracilis,* as shown in the graphic analysis (Figs. 1 and 2) and distribution map (Plate 21), presents two clines: a north-south cline and a large-river to small-river (mainly east-west) cline. The absence of *H. gracilis* from certain portions of river systems is a matter of concern. The species has not been found in the lower Arkansas River and the Rio Grande, nor in sandy tributary creeks in eastern Kansas and Missouri that appear to provide suitable habitat. It has already been noted that *H. g. gulonella* seems to be the ecological equivalent of *Semotilus atromaculatus* in streams in which *S. atromaculatus* is not found. *S. atromaculatus* occurs in creeks of eastern Kansas and Missouri, and may provide interspecific competition that prevents establishment of the flathead chub in these creeks. Regardless of cause, the gaps in distribution of *H. gracilis* tend to limit gene flow.

Many characters used in the separation of the two subspecies are known to be influenced by environmental conditions, especially temperature. Hubbs (1922, 1926, 1941), Schultz (1927), Vladykov (1934), Tåning (1952) and Weisel (1955), among others, have pointed out a correlation between temperature (or developmental rate of fish) and the number of vertebrae, scales, and fin-rays. Likewise, Martin (1949) and Hart (1952) have shown that the proportions of some body-parts vary in response to temperature during early development. In *H. gracilis,* the general nature of the clines found in a majority of characters (but not all characters) suggests a temperature influence. However, temperature-dependent variability that has so far been demonstrated experimentally in fishes is generally of lesser magnitude than the differences distinguishing *H. g. gracilis* and *H. g. gulonella.* To our knowledge, the most extreme differences that have been induced by modification of temperature are those reported for *Salmo trutta* by Tåning (1952:181-182), who states: "Shock treatment produced by especially great changes in temperature (*c.* 10-14° C.), especially during the supersensitive period [of somatic differentiation that fixes vertebral number] may produce . . . a difference of 3-4 vertebrae . . . in offspring of the same parents." The difference cited approximates that which distinguishes natural populations of *H. g. gracilis* and *H. g. gulonella.* Although we cannot assume that the sensitivity of the brown trout is the same as that of the flathead chub, the causative conditions in Tåning's study could scarcely be expected in nature; furthermore, it seems significant that extremely high (as well as extremely low) mean numbers of scales and vertebrae were found at southern localities, and that low mean numbers of scales and vertebrae were found as far north as Wyoming and Montana. We think it likely that temperature does influence the expression of characters in *H. gracilis,* directly in individual development, and indirectly as a selective mechanism in the evolutionary process. The extent to which each kind of influence exists can be proved only by experimental work with both subspecies, which we hope to undertake at a later date.

Other environmental factors that may have selective influence in this species are rate of current, volume of flow, and turbidity. Interaction of these environmental factors could result in genetic fixation of morphological characters through natural selection. The characters that distinguish *H. g. gracilis* from *H. g. gulonella* seem adaptive to life in large rivers and small streams. Evidence that these characters are under limited, direct environmental influence is found among populations in the Arkansas River System. Although populations in the Arkansas River have no continuity with populations of *H. g. gracilis,* upstream-downstream variations like those found in other river systems are apparent, but in lesser degree. The direction of variation in the Arkansas River is the reverse of that in the Platte and other tributaries of the Missouri River. For example, the populations farthest upstream (Florence, Pueblo) have slightly higher mean numbers of lateral line scales than do populations from Kansas, downstream.

A remarkable effect of extreme parasitism in *H. gracilis* has been described by Hubbs (1927). Very young chubs that harbored numerous tapeworms (*Proteocephalus*) had unusually large numbers of lateral-line scales, large eyes, short snouts, small fins, small mouths lacking barbels, and coalescent nares (internarial bridge weak or absent). Some of these abnormalities presumably resulted from retention of larval characteristics of the fish, correlated with the degree of infestation by tapeworms. No teratological adults were found, indicating that severe infections prevent survival to maturity.

H. g. gracilis occurs in three separate river systems (Mackenzie, Saskatchewan, Missouri-Mississippi) from latitude 36° N to 66° N, and longitude 89° W to 123° W. *H. g. gulonella* exists as several seemingly-isolated populations in the upper parts of the Rio Grande, Pecos, South Canadian, Cimarron, Arkansas, Platte, and upper Missouri basins, from latitude 35° N to 48° N, and longitude 97° W to 100° W.

There is evidence of high mobility on the part of both subspecies, based on irregularity of their occurrence in certain localities. Many collections have been made in the Cimarron River in the vicinity of Kenton, Oklahoma, from 1925 to the present, but only one of these (in 1957) contained flathead chubs. Bait dealers who seine the South Canadian River in Dewey County, Oklahoma, have taken flathead chubs in abundance in some seasons, but not at all in others. Seasonal variation in abundance in the lower Vermillion River, South Dakota (Underhill, 1959:100) has been cited, and the number collected in the lower Kansas River near Lawrence has varied similarly. Many rivers occupied by *H. g. gulonella* (and by intergrades) are intermittent, and in some years their sand-filled channels become wholly dry for many miles. These factors probably promote mixing of the two subspecies, and may account, over long periods of time, for the wide dispersal of *H. g. gulonella* in the Missouri Basin. Flathead chubs are known from Pleistocene beds at Doby Springs, Oklahoma (the Doby Springs local fauna) (Smith, 1958:177). Drainage connections between the Arkansas, Kansas and Platte river systems existed in Kansan and Nebraskan times (Frye and Leonard, 1952:189-190). Populations that have subsequently become isolated in those rivers could be accounted for in this way. Flathead chubs could have entered the Rio Grande-Pecos system by stream-capture from the Arkansas System, in northeastern New Mexico or southern Colorado. *H. g. gracilis* undoubtedly entered the Saskatchewan and Mackenzie basins from the upper Missouri Basin, following glacial retreat (Walters, 1955:347).

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Studies of American Hylid Frogs, V

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WILLIAM E. DUELLMAN

Field studies on hylid frogs in southern México and northern Central America have resulted in the collection of numerous specimens of *Ptychohyla,* a genus of hylid frogs heretofore poorly represented in museum collections. Experience with the living frogs in their natural habitats has been helpful in defining the species and in formulating ideas concerning their relationships.

Taylor (1944) proposed the generic name *Ptychohyla* for a new species of frog, *Ptychohyla adipoventris* [= *Ptychohyla leonhardschultzei* (Ahl)—*fide* Duellman, 1960] from Agua del Obispo, Guerrero. Taylor defined the genus as having large ventrolateral glands and horny nuptial spines in males. Stuart (1954:169) discussed the generic characters and pointed out that both the ventrolateral glands and horny nuptial spines were seasonal in their development, being found only in breeding males. Stuart then went on to describe *Ptychohyla schmidtorum,* a species characterized by the absence of horny nuptial spines in breeding males. My investigations of these frogs have revealed the presence of two groups of species. In both groups breeding males have large ventrolateral glands, but the two groups are easily separated by four characters. The first group contains, among others, *Ptychohyla leonhardschultzei, euthysanota, spinipollex,* and another species in the Mesa Central of Chiapas to which I tentatively apply the name *Ptychohyla macrotympanum* (Tanner), 1957. This group of species is characterized by horny nuptial spines in breeding males, presence of a tarsal fold, a call consisting of a single long note, and tadpoles having lips not greatly expanded. The second group, as recognized here, is characterized by the absence of horny nuptial spines in breeding males, lack of a tarsal fold, a call consisting of a series of short notes, and tadpoles having greatly expanded lips. In this group belong *Ptychohyla schmidtorum* and the two species described below.

Only the descriptions of the new species are given in this paper; detailed comparisons, descriptions of osteological features, analyses of calls, and discussions of relationships are reserved for a forthcoming review of the entire genus.

In the spring of 1959, collections of amphibians and reptiles were made in the cloud forests on the northern slopes of the Sierra Madre Oriental in northern Oaxaca. Among the hylids found, two specimens of a heretofore unnamed species of *Ptychohyla* have brilliant red flash-colors on the groin and thighs; in allusion to these fiery colors I propose that this species be named:

Ptychohyla ignicolor new species

(Plate 25, Fig. 1)

Holotype.—University of Michigan Museum of Zoology No. 119603, from a stream 6 kilometers south of Vista Hermosa, Oaxaca, México (1865 meters); obtained on March 31, 1959, by Thomas E. Moore. Original Number WED 14159.

Paratype.—UMMZ 119602 from Vista Hermosa, Oaxaca (1500 meters); obtained on March 30, 1959, by William E. Duellman.

Diagnosis.—A species of the *schmidtorum*-group of *Ptychohyla* differing from other known members of the group in having the diameter of the tympanum less than one-half the diameter of the eye, no white spot below the eye, no lateral light stripe, bright green dorsum in life and red flash-colors on groin and thighs.

Description of Holotype.—Adult male having a snout-vent length of 30.0 mm.; tibia length, 14.6 mm.; tibia length/snout-vent length, 48.7 per cent; foot length (measured from proximal edge of inner metatarsal tubercle to tip of longest toe), 12.3 mm.; head length, 9.2 mm.; head length/snout-vent length, 32.3 per cent; head width, 9.3 mm.; head width/snout-vent length, 31.0 per cent; diameter of eye, 3.2 mm.; diameter of tympanum, 1.3 mm.; tympanum/eye, 40.6 per cent. Snout in lateral profile square, in dorsal profile obtusely rounded; canthus pronounced; loreal region slightly concave; lips moderately flaring; top of head flat; nostrils protuberant; internarial distance, 2.8 mm.; interorbital distance, 3.3 mm., much broader than width of eyelid, 2.8 mm. A heavy dermal fold from posterior corner of eye above tympanum to insertion of forelimb, covering upper edge of tympanum; tympanum elliptical, its greatest diameter equal to its distance from eye. Forearm robust with a distinct fold on wrist; pollex moderately enlarged without nuptial spines; second and fourth fingers equal in length; subarticular tubercles round; none is bifid; disc of third finger slightly larger than tympanum; no web between first and second fingers; vestige of web between other fingers. Heels overlap when hind limbs adpressed; tibiotarsal articulation extends to anterior corner of eye; no tarsal fold; inner metatarsal tubercle large, flat, and elliptical; outer metatarsal tubercle near inner one and triangular; subarticular tubercles round; length of digits from shortest to longest 1-2-5-3-4; toes about one-half webbed; discs smaller on toes than on fingers. Anal opening directed posteriorly at upper level of thighs; no anal flap; pair of large tubercles below anal opening; small tubercles ventral and lateral to these. Skin of dorsum and ventral surfaces of limbs smooth, that of throat and belly granular. Ventrolateral glands noticeably thickened,

PLATE 25

FIG. 1. Paratype of *Ptychohyla ignicolor* (UMMZ 119602). × 3.

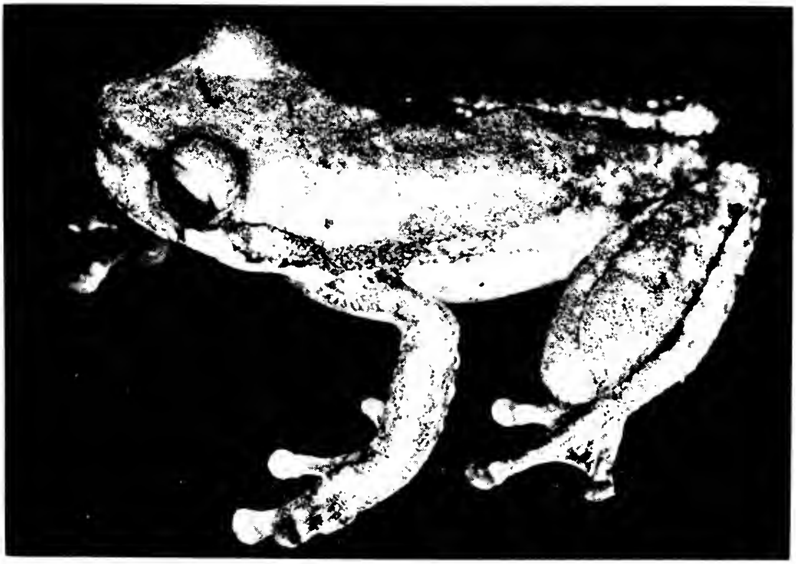

FIG. 2. Holotype of *Ptychohyla chamulae* (KU 58063). × 3.

extending from axilla nearly to groin and only narrowly separated medially on chest. Skin of anterior part of chin thickened and glandular. Tongue cordiform, shallowly notched behind and only slightly free posteriorly; vomerine teeth 0-3, situated on rounded elevations between somewhat larger, round inner nares; openings to vocal sac large, one situated along posterior margin of each mandibular ramus.

Color (in alcohol) dull brown above with irregular dark brown blotches; dorsal surfaces of limbs brown with narrow darker brown transverse bars; posterior surfaces of thighs cream-color with brown spots and mottling; groin and dorsal surfaces of first and second toes white; belly cream-colored; glandular areas orange-brown; chest and chin having black spots. Ventral surfaces of hind limbs and first toes cream-colored; undersides of other toes and soles of feet brown.

Color (in life) uniform bright green above; venter pale creamy yellow; anterior and posterior surfaces of thighs, ventral surfaces of shanks, anterior surfaces of tarsi and upper proximal surfaces of first three toes red; iris pale golden color.

The paratype is an adult male, having a snout-vent length of 26.3 mm., and agrees with the holotype in proportions. The ventrolateral glands are less extensive and the chin less spotted than in the holotype.

Comparisons: Both *Ptychohyla schmidtorum* and the species described below differ from *P. ignicolor* in lacking red flash-colors and in having a white spot below the eye. *Ptychohyla ignicolor* also differs in having a small tympanum. As stated above, these species can be distinguished from the rest of the genus by the absence of a tarsal fold and absence of horny nuptial spines in breeding males.

Remarks: The holotype was found on a moss-covered log over a stream in dense cloud forest by day. The paratype was calling at night from a low herb at the edge of a small stream in the cloud forest. Nearby a *Ptychohyla leonhard-schultzei* was calling.

Along two cascading mountain streams in cloud forest on the northern slopes of the Mesa Central in central Chiapas numerous specimens of a distinctive species of *Ptychohyla* were found in association with two species of *Hyla* and two of *Plectrohyla.* The first specimen of this new species of *Ptychohyla* was discovered by Dale L. Hoyt, who found the frog on a rock at midday. At night on August 5, 1960, numerous individuals were found calling from leaves of plants growing on the slopes of the ravine by the streams. None was more than two meters above the ground. Tadpoles were found in the fast-flowing stream, where they were holding onto rocks with their mouths. Little is known of the herpetofauna of these mountains that are the home of the Chamula Indians. Since the little frog described here comes from the land of the Chamulas, I propose that it be named:

Ptychohyla chamulae new species

(Plate 25, Fig. 2)

Holotype.—University of Kansas Museum of Natural History No. 58063, from a stream above (6.2 kilometers by road south) Rayón Mescalapa, Chiapas, México (1690 meters); one of a series collected on August 5, 1960, by William E. Duellman, Dale L. Hoyt, and John Wellman. Original No. WED 17327.

Paratypes.—KU Nos. 58064-58073 collected with the holotype.

Diagnosis.—A species of the *schmidtorum*-group of *Ptychohyla* differing from other known members of the group in having the following combination of characters: diameter of tympanum not noticeably less than half that of eye; white spot below eye; white lateral stripe on body anteriorly; dorsum bright green in life; thighs yellowish brown.

Description of Holotype.—Adult male having snout-vent length of 27.3 mm.; tibia length, 12.8 mm.; tibia length/snout-vent length, 48.7 per cent; foot length (measured from proximal edge of inner metatarsal tubercle to tip of longest toe), 10.8 mm.; head length, 9.2 mm.; head length/snout-vent length, 33.7 per cent; head width, 9.0 mm.; head width/snout-vent length, 30.9 per cent; diameter of eye, 2.8 mm.; diameter of tympanum, 1.4 mm.; tympanum/eye, 50.0 per cent. Snout in lateral profile nearly square, slightly rounded above; in dorsal profile bluntly squared; canthus pronounced; loreal region concave; lips thick, rounded, and flaring; nostrils protuberant; internarial distance, 2.3 mm.; top of head flat; interorbital distance, 3.3 mm.; much broader than width of eyelid, 2.4 mm. A thin dermal fold from posterior corner of eye above tympanum to insertion of forelimb, covering upper edge of tympanum; tympanum nearly round, its diameter equal to its distance from eye. Forearm slender lacking distinct fold on wrist; a row of low, rounded tubercles on ventrolateral surface of forearm; pollex moderately enlarged without nuptial spines; second and fourth fingers equal in length; subarticular tubercles round, none bifid; discs small, that of third finger noticeably smaller than tympanum; no web between first and second fingers; vestige of web between other fingers. Heels overlap when hind limbs adpressed; tibiotarsal articulation reaches to middle of eye; no tarsal fold; inner metatarsal tubercle large, flat, and elliptical; outer metatarsal tubercle slightly more distal than inner, small, and elliptical; subarticular tubercles round; length of digits from shortest to longest 1-2-5-3-4; third and fifth toes webbed to base of disc; fourth toe webbed to base of penultimate phalanx; discs smaller on toes than on fingers. Anal opening directed posteriorly at upper level of thighs; no anal flap; pair of large tubercles below anal opening and a slightly smaller pair farther below. Skin of dorsum and ventral surfaces of forelimbs and shanks smooth; that of throat, belly, and ventral surfaces of thighs granular. Ventrolateral glands well developed, not reaching axilla or groin and broadly separated midventrally. Skin of anterior part of chin glandular. Tongue cordiform, shallowly notched behind and only slightly free posteriorly; vomerine teeth 2-2, situated on small triangular elevations between large, ovoid inner nares; openings to vocal sac large, one situated along inner posterior edge of each mandibular ramus.

Color (in alcohol) dark purplish brown on dorsal surfaces of head, body, and shanks; thighs brown above and yellowish tan posteriorly; white stripe extending from below eye above forearm to mid-flank. Ventral surfaces creamy white; ventrolateral glands orange-tan flecked with dark brown; edge of lower lip with dark brown spots; narrow white line on upper lip; palms white and soles brown.

Color (in life) uniform dark bright green above with creamy white bar below eye; lateral stripe silvery white; ventral surfaces deep yellow; posterior surfaces of thighs yellow brown; iris reddish bronze.

Variation.—Sixteen adult males are available; these have snout-vent lengths of 26.3 to 28.5 mm. (average, 27.6 mm.). The tympanum/eye ratio is 48.2 to 58.6 per cent (average, 53.2 per cent). The number of vomerine teeth varies from four to six. The extent of the ventrolateral glands is variable. In five specimens the glands nearly meet midventrally; in two others the glands include the axillary region; in none do the glands extend into the groin. In other structural details there is no noticeable variation.

The greatest variation in color pattern is found in the lateral stripe. The pale spot or bar below the eye is present in all specimens; in one individual there is no lateral stripe; in three the stripe extends posteriorly only to above the forearm, in two to the mid-flank, and in the others to the groin.

Although all of the males were bright uniform green above when collected at night as they were calling, some changed color later. In these individuals the dorsum became a somewhat paler green with faint irregular yellowish tan blotches.

The one available female (UMMZ 121399) has a snout-vent length of 30.3 mm. and a tympanum/eye ratio of 52.8 per cent, and is colored like the males. The tubercles by the anal opening are placed irregularly and do not consist of two pairs below the opening. There are no ventrolateral glands, glandular area on the chin, or enlarged prepollex.

Comaprisons.—*Ptychohyla chamulae* resembles *P. schmidtorum* in color pattern and body proportions, but the ground color of *schmidtorum* is chocolate brown and not green as in *chamulae.* Also, in *schmidtorum* the webbing and posterior surfaces of the thighs are pale cream-color in preserved specimens as contrasted with tan in *chamulae.* In living *schmidtorum* the iris is bright red, not reddish bronze as in *chamulae.* The ventrolateral glands in *schmidtorum* more closely approximate one another midventrally than in *chamulae.* It is conceivable that these populations are subspecifically related; *schmidtorum* occurs in the same kind of habitat as does *chamulae,* but is known only from the Pacific slopes of southeastern Chiapas and southwestern Guatemala, whereas *chamulae* is known only from the Atlantic slopes of the Mesa Central in north-central Chiapas. Both of these species differ from *Ptychohyla ignicolor* in having a relatively larger tympanum, more webbing on the foot, different arrangement of anal tubercles, and different coloration.

Description of Tadpole.—Six tadpoles having fully developed mouth parts have body lengths of 5.5 to 11.9 mm. and total lengths of 17.3 to 44.0 mm. The following description is based on a tadpole (KU 58199) having small hind limbs, a body length of 10.5 mm., and a total length of 39.0 mm. Body ovoid, only slightly flattened dorsally and ventrally (Fig. 1); body only slightly deeper than wide; eyes directed dorsolaterally and slightly protuberant; nostrils small. Tail long and slender; greatest depth of tail-musculature two-thirds greatest depth of tail-fin; tail-musculature extending nearly to tip of tail-fin.

Mouth directed anteroventrally; thin fleshy lips greatly expanded and forming large suckerlike disc; width of mouth greater than width of snout and nearly as wide as body. Outer edge of lips having small papillae; inner surface of mouth smooth; scattered large papillae, seemingly in rows, around teeth and beak (Fig. 2). Tooth rows 3/3; the upper rows subequal in length; upper rows one and three interrupted medially; lower rows one and two about equal in length to upper rows; third lower row short. Upper beak heavy and horn-covered.

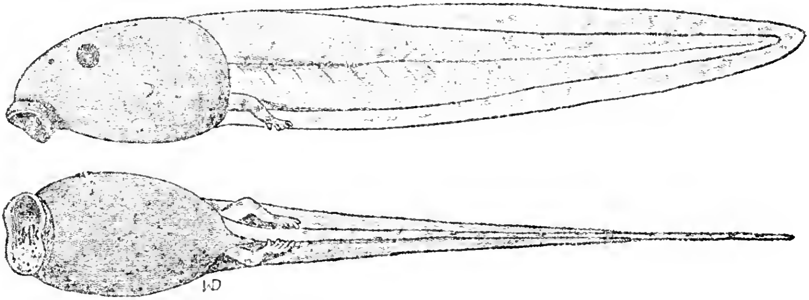

FIG. 1. Tadpole of *Ptychohyla chamulae* (KU 58199). × 2.5.

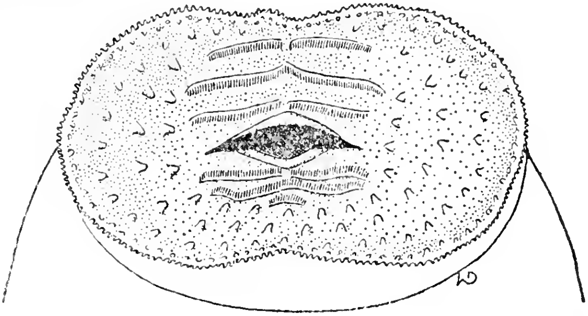

FIG. 2. Mouthparts of tadpole of *Ptychohyla chamulae* (KU 58199). × 16.

Color (in alcohol) dark brown over entire body and tail-musculature; a white area near base of tail, and a dark streak on anterior one-fourth of tail; tail-fin transparent having brown blotches.

Remarks.—Five metamorphosing tadpoles and juveniles (KU 58074, 58234-8) were found at night on vegetation by streams. Of two completely metamorphosed young each has a snout-vent length of 15.7 mm. Another having a snout-vent length of 16.2 mm. has a tail stub 2 mm. long and a completely metamorphosed mouth. Two others have snout-vent lengths of 13.6 and 14.1 mm. and tail lengths of 11.5 and 8.1 mm. respectively; in these the mouth parts are incompletely metamorphosed. The single female available (UMMZ 121399) contains approximately 60 ovarian eggs, the largest of which are about 2.5 mm. in diameter.

Referred Specimens.—Chiapas: 6.2 km. S of Rayón Mescalapa, KU 58063-74, 58199 (1 tadpole), 58234-8; 5.6 km. S of Rayón Mescalapa, KU 58062, 58200 (5 tadpoles); 11.4 mi. N of Pueblo Nuevo Solistahuacán, UMMZ 121395-9. The specimens listed last were collected along a stream between Pueblo Nuevo Solistahuacán and Rayón Mescalapa, which, according to Floyd L. Downs, is probably the same stream listed above as 5.6 km. S of Rayón Mescalapa.

Acknowledgments

I take this opportunity to thank Dale L. Hoyt, Thomas E. Moore, and John Wellman, who ably assisted in collecting and studying these frogs in the field. I am indebted to Floyd L. Downs for permission to include specimens collected by him and John Winklemann. My studies on hylid frogs are supported by the National Science Foundation (Grant G 9827).

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August 11, 1961

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BY

JAMES EVERETT DEACON

(Joint Contribution from the State Biological Survey and
the Forestry, Fish, and Game Commission)

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13. A new cottontail (Sylvilagus floridanus) from northeastern Mexico. By Rollin H. Baker. Pp. 609-612. April 8, 1955.
14. Taxonomy and distribution of some American shrews. By James S. Findley. Pp. 613-618. June 10, 1955.
15. The pigmy woodrat, Neotoma goldmani, its distribution and systematic position. By Dennis G. Rainey and Rollin H. Baker. Pp. 619-624, 2 figures in text. June 10, 1955.

Index. Pp. 625-651.

(Continued on inside of back cover)

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CONTENTS

TABLES

INTRODUCTION

This report concerns the ability of fish-populations in the Neosho and Marais des Cygnes rivers in Kansas to readjust to continuous stream-flow following intermittent conditions resulting from the severest drought in the history of the State.

The variable weather in Kansas (and in other areas of the Great Plains) markedly affects its flora and fauna. Weaver and Albertson (1936) reported as much as 91 per cent loss in the basal prairie vegetative cover in Kansas near the close of the drought of the 1930's. The average annual cost (in 1951 prices) of floods in Kansas from 1926 to 1953 was $35,000,000. In the same period the average annual loss from the droughts of the 1930's and 1950's was $75,000,000 (in 1951 prices), excluding losses from wind- and soil-erosion. Thus, over a period of 28 years, the average annual flood-losses were less than one-half the average annual drought-losses (Foley, Smrha, and Metzler, 1955:9; Anonymous, 1958:15).

Weather conditions in Kansas from 1951 to 1957 were especially noteworthy: 1951 produced a bumper crop of climatological events significant to the economy of the State. Notable among these were: Wettest year since beginning of the state-wide weather records in 1887; highest river stages since settlement of the State on the Kansas River and on most of its tributaries, as well as on the Marais des Cygnes and on the Neosho and Cottonwood. The upper Arkansas and a number of smaller streams in western Kansas also experienced unprecedented flooding (Garrett, 1951:147). This period of damaging floods was immediately followed by the driest five-year period on record, culminating in the driest year in 1956 (Garrett, 1958:56). Water shortage became serious for many communities. The Neosho River usually furnishes adequate quantities of water for present demands, but in some years of drought all flow ceases for several consecutive months. In 1956-'57, the city of Chanute, on an emergency basis, recirculated treated sewage for potable supply (Metzler *et al.*, 1958). The water shortage in many communities along the Neosho River became so serious that a joint project to pump water from the Smoky Hill River into the upper Neosho was considered, and preliminary investigations were made. If the drought had continued through 1957, this program might have been vigorously promoted. Data on stream-flow in the Neosho and Marais des Cygnes (1951-'59) are presented in Tables 1-4.

These severe conditions provided a unique opportunity to gain insight into the ability of several species of fish to adjust to marked

TABLE 1. STREAM-FLOW IN CUBIC FEET PER SECOND, NEOSHO RIVER NEAR COUNCIL GROVE, KANSAS. DRAINAGE AREA: 250 SQUARE MILES

WATER-YEAR *	Average flow	Maximum	Minimum
1951	498.0	121,000	3.0
1952	82.1	4,850	.7
1953	5.37	202	.1
1954	8.53	2,720	.1
1955	31.2	6,480	0
1956	10.1	5,250	0
1957	68.5	12,300	0
1958	131.0	5,360	.8
1959	114.0	7,250	8.5

* (Oct. 1-Sept. 30, inclusive)

TABLE 2. STREAM-FLOW IN CUBIC FEET PER SECOND, NEOSHO RIVER NEAR PARSONS, KANSAS. DRAINAGE AREA: 4905 SQUARE MILES.

WATER-YEAR *	Average flow	Maximum	Minimum
1951	8,290	410,000	124.0
1952	2,021	20,500	20.0
1953	173	4,110	.3
1954	430	27,900	.1
1955	645	18,600	0
1956	180	6,170	0
1957	1,774	25,000	0
1958	3,092	27,200	78.0
1959	1,609	22,600	139.0

* (Oct. 1-Sept. 30, inclusive)

TABLE 3. STREAM-FLOW IN CUBIC FEET PER SECOND, MARAIS DES CYGNES RIVER NEAR OTTAWA, KANSAS. DRAINAGE AREA: 1,250 SQUARE MILES.

WATER-YEAR	Average flow	Maximum	Minimum
1951	2,113	142,000	25.0
1952	542	12,000	.2
1953	36.5	2,690	.2
1954	73.6	5,660	.5
1955	75.7	5,240	.7
1956	26	1,590	.7
1957	442	11,200	.7
1958	775	9,130	5.6

changes in their environment. For this reason, and because of a paucity of information concerning stream-fish populations in Kansas, the study here reported on was undertaken.

TABLE 4. STREAM-FLOW IN CUBIC FEET PER SECOND, MARAIS DES CYGNES RIVER AT TRADING POST, KANSAS. DRAINAGE AREA: 2,880 SQUARE MILES.

WATER-YEAR	Average flow	Maximum	Minimum
1951	5,489	148,000	36.0
1952	1,750	20,400	3.0
1953	261	7,590	0
1954	334	12,500	0
1955	786	16,100	.2
1956	202	10,000	0
1957	871	14,700	0
1958	2,453	20,400	120.0
*1959	750	10,900	3.4

* The gaging station was moved a short distance downstream to the Kansas-Missouri state line.

DESCRIPTION OF NEOSHO RIVER

The Neosho River, a tributary of Arkansas River, rises in the Flint Hills of Morris and southwestern Wabaunsee counties and flows southeast for 281 miles in Kansas, leaving the state in the extreme southeast corner (Fig. 1). With its tributaries (including Cottonwood and Spring rivers) the Neosho drains 6,285 square miles in Kansas and enters the Arkansas River near Muskogee, Oklahoma (Schoewe, 1951:299). Upstream from its confluence with Cottonwood River, the Neosho River has an average gradient of 15 feet per mile. The gradient lessens rapidly below the mouth of the Cottonwood, averaging 1.35 feet per mile downstream to the State line (Anonymous, 1947:12). The banks of the meandering, well-defined channel vary from 15 to 50 feet in height and support a deciduous fringe-forest. The spelling of the name originally was "Neozho," an Osage Indian word signifying "clear water" (Mead, 1903:216).

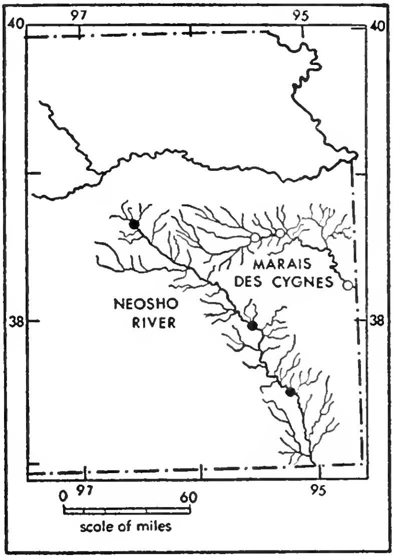

FIG. 1. Neosho and Marais des Cygnes drainage systems. Dots and circles indicate collecting-stations.

Neosho River, Upper Station.—Two miles north and two miles west of Council Grove, Morris County, Kansas (Sec. 32 and 33, T. 15 S., R. 8 E.) (Pl. 28, Fig. 2, and Pl. 29, Fig. 1). Width 20 to 40 feet, depth to six feet, length of study-area one-half mile (one large pool plus many small pools connected by riffles), bottom of mud, gravel, and rubble. Muddy banks 20 to 30 feet high.

According to H. E. Bosch (landowner) this section of the river dried completely in 1956, except for the large pool mentioned above. This section was intermittent in 1954 and 1955; it again became intermittent in the late summer of 1957 but not in 1958 or 1959.

A second section two miles downstream (on land owned by Herbert White) was studied in the summer of 1959 (Sec. 3 and 10,

T. 16 S., R. 8 E.) (Pl. 29, Fig. 2 and Pl. 30, Figs. 1 and 2). This section is 20 to 60 feet in width, to five feet in depth, one-half mile in length (six small pools with intervening riffles bounded upstream by a low-head dam and downstream by a long pool), having a bottom of gravel, rubble, bedrock, and mud, and banks of mud and rock, five to 20 feet in height.

Neosho River, Middle Station.—One mile east and one and one-half miles south of Neosho Falls, Woodson County, Kansas (Sec. 3 and 4, T. 24 S., R. 17 E.) (Pl. 26, Fig. 1). Width 60 to 70 feet, depth to eleven feet, length of study-area two miles (four large pools with connecting riffles), bottom of mud, gravel and rock. Mud and rock banks 30 to 40 feet high.

According to Floyd Meats (landowner) this section of the river was intermittent for part of the drought.

Neosho River, Lower Station.—Two and one-half miles west, one-half mile north of Saint Paul, Neosho County, Kansas (Sec. 16, T. 29 S., R. 20 E.). Width 100 to 125 feet, depth to ten feet, length of study-area one mile (two large pools connected by a long rubble-gravel riffle), bottom of mud, gravel, and rock. Banks, of mud and rock, 30 to 40 feet high (Pl. 26, Fig. 2).

This station was established after one collection of fishes was made approximately ten miles upstream (Sec. 35, T. 28 S., R. 19 E.). The second site, suggested by Ernest Craig, Game Protector, provided greater accessibility and a more representative section of stream than the original locality.

DESCRIPTION OF MARAIS DES CYGNES RIVER

The Marais des Cygnes River, a tributary of Missouri River, rises in the Flint Hills of Wabaunsee County, Kansas, and flows generally eastward through the southern part of Osage County and the middle of Franklin County. The river then takes a southeasterly course through Miami County and the northeastern part of Linn County, leaving the state northeast of Pleasanton. With its tributaries (Dragoon, Salt, Pottawatomie, Bull and Big Sugar creeks) the river drains 4,360 square miles in Kansas (Anonymous, 1945:23), comprising the major part of the area between the watersheds of the Kansas and Neosho rivers. The gradient from the headwaters to Quenemo is more than five feet per mile, from Quenemo to Osawatomie 1.53 feet per mile, and from Osawatomie to the State line 1.10 feet per mile (Anonymous, 1945:24). The total length is approximately 475 miles (150 miles in Kansas). The river flows in a highly-meandering, well-defined channel that has been entrenched from 50 to 250 feet (Schoewe, 1951:294). "Marais des Cygnes" is of French origin, signifying "the marsh of the swans."

Marais des Cygnes River, Upper Station.—One mile south and one mile west of Pomona, Franklin County, Kansas (Sec. 12, T. 17 S., R. 17 E.) (Pl. 27, Fig. 1). Width 30 to 40 feet, depth to six feet, length of study-area one-half mile (three large pools with short connecting riffles), bottom of mud and bedrock. Mud banks 30 to 40 feet high.

According to P. Lindsey (landowner) this section of the river was intermittent for most of the drought. Flow was continuous in 1957, 1958 and 1959.

There are four low-head dams between the upper and middle Marais des Cygnes stations.

Marais des Cygnes River, Middle Station.—One mile east of Ottawa, Franklin County, Kansas (Sec. 6, T. 17 S., R. 20 E.) (Pl. 27, Fig. 2). Width 50 to 60 feet, depth to eight feet, length of study-area one-half mile (one large pool plus a long riffle interrupted by several small pools), bottom of mud, gravel, and rock. Mud and sand banks 30 to 40 feet high.

This section of the river was intermittent for much of the drought. In the winter of 1957-'58 a bridge was constructed over this station as a part of Interstate Highway 35. Because of this construction many trees were removed from the stream-banks, the channel was straightened, a gravel-bottomed riffle was rerouted, and silt was deposited in a gravel-bottom pool.

Marais des Cygnes River, Lower Station.—At eastern edge of Marais des Cygnes Wildlife Refuge, Linn County, Kansas (Sec. 9, T. 21 S., R. 25 E.). Width 80 to 100 feet, depth to eight feet, length of study-area one-half mile (one large pool plus a long riffle interrupted by several small pools), bottom of mud, gravel, and rock. Mud banks 40 to 50 feet high.

This section of the river ceased to flow only briefly in 1956.

METHODS

Electrical Fishing Gear

The principal collecting-device used was a portable (600-watt, 110-volt, A. C.) electric shocker carried in a 12-foot aluminum boat. Two 2 x 2-inch wooden booms, each ten feet long, were attached to the front of the boat in a "V" position so they normally were two feet above the surface of the water. A nylon rope attached to the tips of the booms held them ten feet apart. Electrodes, six feet long, were suspended from the tip and center of each boom, and two electrodes were suspended from the nylon rope. The electrodes extended approximately four feet into the water. Of various materials used for electrodes, the most satisfactory was a neoprene-core, shielded hydraulic hose in sections two feet long. These lengths could be screwed together, permitting adjustment of the length of the electrodes with minimum effort. At night, a sealed-beam automobile headlight was plugged into a six-volt D. C. outlet in the generating unit and a Coleman lantern was mounted on each gunwale to illuminate the area around the bow and along the sides of the boat (Pl. 3a). In late summer, 1959, a 230-volt, 1500-watt generating unit, composed of a 115-volt, 1500-watt Homelite generator was used. It was attached to a step-up transformer that converted the current to 230 volts. The same booms described above were used with the 230-volt unit, with single electrodes at the tip of each boom.

A 5.5-horsepower motor propelled the boat, and the stunned fish were collected by means of scap nets. Fishes seen and identified but not captured also were recorded. On several occasions fishes were collected by placing a 25-foot seine in the current and shocking toward the seine from upstream.

The shocker was used in daylight at all six stations in the three years, 1957-'59. Collections were made at night in 1958 and 1959 at the middle Neosho station and in 1959 at the lower Neosho station.

Seines

Seines of various lengths (4, 6, 12, 15, 25 and 60 feet), with mesh-sizes varying from bobbinet to one-half inch, were used. The 4-, 12-, and 25-foot seines were used in the estimation of relative abundance by taking ten hauls with each seine, recording all species captured in each haul, and making a total count of all fish captured in two of the ten hauls. The two hauls to be counted were chosen prior to each collection from a table of random numbers. Additional selective seining was done to ascertain the habitats occupied by different species.

Trap, Hoop, and Fyke Nets.—Limited use was made of unbaited trapping devices: wire traps 2.5 feet in diameter, six feet long, covered with one-inch-mesh chicken wire; hoop nets 1.5 feet to three feet in diameter at the first hoop with a pot-mesh of one inch; and a fyke net three feet in diameter at the first hoop, pot-mesh of one inch with wings three feet in length. All of these were set parallel to the current with the mouths downstream. The use of trapping devices was abated because data obtained were not sufficient to justify the effort expended.

Gill Nets

Gill-netting was done mostly in 1959 at the lower Neosho station. Use of gill nets was limited because frequent slight rises in the river caused nets to collect excessive debris, with damage to the nets.

Gill nets used were 125 feet long, six feet deep, with mesh sizes of ¾ inch to 2½ inches. Nets, weighted to sink, were placed at right angles to the current and attached at the banks with rope.

Sodium Cyanide

Pellets of sodium cyanide were used infrequently to collect fish from a moderately fast riffle over gravel bottom that was overgrown with willows, making seining impossible. The pellets were dissolved in a small amount of water, a seine was held in place, and the cyanide solution was introduced into the water a short distance upstream from the seine, causing incapacitated fish to drift into the seine. Most of these fish that were placed in uncontaminated water revived.

Rotenone

Rotenone was used in a few small pools in efforts to capture complete populations. This method was used to check the validity of other methods, and to reduce the possibility that rare species would go undetected. Rotenone was applied by hand, and applications were occasionally supplemented by placing rotenone in a container that was punctured with a small hole and suspended over the water at the head of a riffle draining into the area being poisoned. This maintained a toxic concentration in the pool for sufficient time to obtain the desired kill. Rotenone acts more slowly than cyanide, allowing more of the distressed fish to rise to the surface.

Dyes

Bismark Brown Y was used primarily at the upper Neosho station to stain large numbers of small fish. The dye was used at a dilution of 1:20,000. Fishes were placed in the dye-solution for three hours, then transferred to a live-box in midstream for variable periods (ten minutes to twelve hours) before release.

Determination of Abundance

In the accounts of species that follow, the relative terms "abundant," "common," and "rare" are used. Assignment of one of these terms to each species was based on analysis of data that are presented in Tables 9-16, (pages 402, 403, 404, 405, 408, 410, 411, 414-415, and 416). The number of fish caught per unit of effort with the shocker (Table 10) and with seines (Table 11) constitute the main basis for statements about the abundance of each species at all stations except the upper Neosho station. Species listed in each Table (10 and 11) are those that were taken consistently by the method specified in the caption of the table; erratically, but in large numbers at least once, by that method; and those taken by the method specified but not the other method.

For the species listed in Table 10, the following usually applies: abundant = more than three fish caught per hour; common = one to three fish caught per hour; rare = less than one fish caught per hour.

Tables 12-16 list all fish obtained at the upper Neosho station by means of the shocker, seines, and rotenone.

Names of Fishes

Technical names of fishes are those that seem to qualify under the International Rules of Zoological Nomenclature. Vernacular names are those in Special Publication No. 2 (1960) of the American Fisheries Society, with grammatical modifications required for use in the University of Kansas Publications, Museum of Natural History.

ANNOTATED LIST OF SPECIES

Lepisosteus osseus (Linnaeus)

Long-nosed Gar

The long-nosed gar was abundant at the lower and middle Neosho stations and the lower Marais des Cygnes station. Numbers increased slightly in the period of study, probably because of increased, continuous flow. The long-nosed gar was not taken at the upper Neosho station. At lower stations the fish occurred in many habitats, but most commonly in pools where gar often were seen with their snouts protruding above the water in midstream. Gar commonly lie quietly near the surface, both by day and by night, and are therefore readily collected by means of the shocker. Twice, at night, gar jumped into the boat after being shocked.

Young-of-the-year were taken at the middle and lower stations on both the Neosho and Marais des Cygnes rivers, and all were near shore in quiet water. Many young-of-the-year were seined at the lower Neosho station on 18 June 1959, near the lower end of a gravel-bar in a small backwater-area having a depth of one to three inches, a muddy bottom, and a higher temperature than the mainstream. Forty-three of these young gar averaged 2.1 inches in total length (T. L.).

Comparison of sizes of long-nosed gar taken by means of the shocker and gill nets at the lower and middle Neosho stations revealed that: the average size at each station remained constant from 1957 to 1959; the average size was greater at the lower than at the middle station; and, with the exception of young-of-the-year, no individual shorter than 13 inches was found at the middle station and only one shorter than 16 inches was taken at the lower station (Table 5).

TABLE 5. NUMBERS AND SIZES OF LONG-NOSED GAR CAPTURED BY SHOCKER AND GILL NETS AT THE MIDDLE AND LOWER NEOSHO STATIONS IN 1957, 1958 AND 1959.

Location	Date	Number	Average total length (inches)	Range
Middle Neosho	1957	19	22.2	14-32
Middle Neosho	1958	57	22.2	14-40
Middle Neosho	1959	64	21.6	13-43
Lower Neosho	1957	14	29.4	9-45
Lower Neosho	1958	7	25.3	23-28
Lower Neosho	1959	107	26.2	16-43

Because collecting was intensive and several methods were used, I think that the population of gars was sampled adequately. Wallen (*Fishes of the Verdigris River in Oklahoma,* 1958:29 [mimeographed copy of dissertation, Oklahoma State University]) took large individuals in the mainstream of the Verdigris River in Oklahoma and small specimens from the headwaters of some tributaries. Because I took young-of-the-year at the lower Neosho station, it is possible that long-nosed gar move upstream when small and then slowly downstream to the larger parts of rivers as the fish increase in size. This pattern of size-segregation, according to size of river, merits further investigation.

Ripe, spent, and immature long-nosed gar (38 males and 10 females) were taken in three gill nets, set across the channel, 150 to 500 yards below a riffle, at the lower Neosho station on June 16, 17, and 18, 1959. On 23 June, 1959, 12 males and two females were taken in gill nets set 50, 150, and 400 yards above the same riffle. Operations with the shocker between 24 June and 10 July, 1959, yielded 29 males and three females. The fish were taken from many kinds of habitat in a three-mile section of the river.

Direction of movement as recorded from gill nets shows that of 67 gar taken, 45 had moved downstream and 22 upstream into the nets. Only ten of the above gar were taken from the nets set above the riffle; six of the ten were captured as they moved downstream into the nets.

On one occasion I watched minnows swimming frantically about, jumping out of the water, and crowding against the shore, presumably to avoid a long-nosed gar that swam slowly in and out of view. I have observed similar activity when gar fed in aquaria. Stomachs of a few gar from the Neosho River were examined and found to contain minnows and some channel catfish.

Long-nosed gar have a relatively long life span (Breder, 1936). This longevity and their ability to gulp air probably insure excellent survival through periods of adverse conditions. The population of long-nosed gar probably would not be drastically affected even in the event of a nearly complete failure of one or two successive hatches. Maturity is attained at approximately 20 inches, total length.

Collections at the middle Neosho station in 1958 indicate that the long-nosed gar is more susceptible to capture at night than in daytime (Table 9, p. 402).

Lepisosteus platostomus Rafinesque

Short-nosed Gar

Only one short-nosed gar was taken in 1957, at the lower station on the Neosho River. In 1958 this species was taken at the lower station on the Marais des Cygnes and in 1958 and 1959 at the lower and middle stations on the Neosho. More common in the Neosho than the Marais des Cygnes, *L. platostomus* occurs mainly in large streams and never was taken in the upper portions of either river. Although short-nosed gar were about equally abundant at the middle and lower stations on the Neosho, the average size was greater at the lower station (Table 6). This kind of segregation by size is shared with long-nosed gar, and was considered in the discussion of that species. Short-nosed gar were taken only in quiet water. Both species were collected most efficiently by means of gill nets and shocker. While shocking, I saw many gar only momentarily, as they appeared at the surface, and specific identification was impossible. The total of all gar seen while shocking indicated that gar increased in abundance from 1957 to 1959 (see Tables 5 and 6). Judging from the gar that were identified, the increase was more pronounced in short-nosed gar than in long-nosed gar.

At the lower Neosho station in 1959, two ripe females and one spent female were taken in gill nets (16, 23 and 17 June, respectively) and were moving downstream when caught. No males were taken in the nets. Subsequently, by means of the shocker (26 June-8 July), two spent and two ripe males were captured in quiet water of the mainstream that closely resembled areas in which the gill nets were set. No females were taken by means of the shocker.

TABLE 6. NUMBERS AND SIZES OF SHORT-NOSED GAR CAPTURED BY SHOCKER AND GILL NETS AT THE MIDDLE AND LOWER NEOSHO STATIONS IN 1958 AND 1959.

Location	Date	Number	Average total length (inches)	Range
Middle Neosho	1958	6	14.9	13.9-15.5
Middle Neosho	1959	9	13.6	11.0-16.0
Lower Neosho	1958	3	21.0	20.3-21.6
Lower Neosho	1959	5	21.3	18.0-24.5

Dorosoma cepedianum (LeSueur)

Gizzard Shad

Gizzard shad declined in abundance from 1957 to 1959. The largest population occurred at the middle station on the Marais des Cygnes in 1957. Shad were mainly in quiet water; often, when the river-level was high, I found them predominately in backwaters or in the mouths of tributary streams. Examination of nine individuals, ranging in size from seven inches to 13.5 inches T. L., indicated that maturity is reached at 10 to 11 inches T. L. Spawning probably occurred in late June in 1959 ("ripe" female caught on 26 June); young-of-the-year were first recorded in mid-July.

Cycleptus elongatus (LeSueur)

Blue Sucker

The blue sucker was taken rarely in the Neosho River and not at all in the Marais des Cygnes in my study. Cross (personal communication) obtained several blue suckers in collections made in the mainstream of the Neosho River in 1952; both young and adults occupied swift, deep riffles. The species seemingly declined in abundance during the drought, and at the conclusion of my study (1959) had not regained the level of abundance found in 1952.

Ictiobus cyprinella (Valenciennes)

Big-mouthed Buffalo

Big-mouthed buffalo were found in quiet water at all stations, but were rare. A ripe female, 21.5 inches long, was taken at the lower station on the Neosho on 16 June, 1959.

Ictiobus niger (Rafinesque)

Black Buffalo
and

Ictiobus bubalus (Rafinesque)

Small-mouthed Buffalo

Black buffalo were not taken at the upper station on the Neosho and were rare at other stations. Small-mouthed buffalo were taken at all stations and were common in the lower portions of the two streams. While the shocker was being used, buffalo were often seen only momentarily, thereby making specific identification impossible; both species were frequently taken together, and for this reason are discussed as a unit. Both species maintained about the same level of abundance throughout my study.

The two species were taken most often in the deeper, swifter currents of the mainstream, but were sometimes found in pools, creek-mouths and backwaters. On several occasions in the summer of 1959, buffalo were seen in shallow parts of long, rubble riffles, with the dorsal or caudal fins protruding above the surface. Ernest Craig, game protector, said buffalo on such riffles formerly provided much sport for gig-fishermen. He stated that the best catches were made at night because the fish were less "spooky" then than in daytime. In my collections made by use of the shocker, buffalo were taken more frequently at night (Table 9, p. 402).

On 19 June, 1959, I saw many buffalo that seemed to be feeding as they moved slowly upstream along the bottom of a riffle. The two species, often side by side, were readily distinguishable underwater. Small-mouthed buffalo appeared to be paler (slate gray) and more compressed than the darker black buffalo. To test the reliability of underwater identifications, I identified all individuals prior to collection with a gig. Correct identification was made of all fish collected on 19 June. The smallest individual obtained in this manner was 18.5 inches T. L. On 26 August, 1959, 16 small-mouthed buffalo were captured and many more were seen while the shocker was in use in the same riffle for one hour and ten minutes. One small-mouthed buffalo was caught while the shocker was being used in the pool below that riffle for one hour and fifty minutes. No black buffalo were taken on 26 August.

Spawning by buffalo was not observed but probably occurred in spring; all mature fish in my earliest collections (mid-June of each year) were spent. Small-mouthed buffalo reach maturity at approximately 14 inches T. L.

Carpiodes carpio carpio (Rafinesque)

River Carpsucker

River carpsucker were abundant throughout the study at all stations. Adults were taken most frequently in quiet water, but depth and bottom-type varied. The greatest concentrations occurred in mouths of creeks during times of high water; occasionally, large numbers were taken in a shallow backwater near the head of a riffle at the middle Neosho station. River carpsucker feed on the bottom but seem partly pelagic in habit. They were taken readily by means of the shocker and gill nets at all depths. The population of *C. carpio* in the Neosho River probably was depleted by drought, although many individuals survived in the larger pools.

When stream-flow was restored, carpsucker probably moved rapidly upstream but had a scattered distribution in 1957. Trautman (1957:239) states that in the Scioto River, Ohio, river carpsucker moved upstream in May and downstream in late August and early September. Numbers found at the middle and lower Neosho stations suggest similar movements in the Neosho River in 1957. In midsummer they were common at the middle station but rare at the lower station; however, they became abundant at the lower station in November. The abundance in late fall at the lower Neosho station might have resulted either from downstream migration or from continued upstream movement into thinly populated areas. No indication of seasonal movement was found in 1958 or 1959.

River carpsucker reach maturity at approximately 11 inches T. L., and spawning occurs in May or June. A ripe male was taken from a gravel-bottomed riffle, three feet deep, at the middle station on the Neosho station on 10 June 1959.

The size-distribution of individuals taken at the middle Neosho station is presented in Fig. 2. The collection in early July of 1958 indicates that one size-group (probably the 1957 year-class) had a median length of approximately seven inches. The modal length of this group was nine inches in June, 1959. A second, predominant size-group (Fig. 2) seemed to maintain almost the same median size throughout all the collection periods, although specimens taken in the spring of 1959 were slightly smaller than those obtained in 1958. This apparent stability in size may have been due to an influx of the faster-growing individuals from a smaller size-group, coupled with mortality of most individuals more than 14 inches in length.

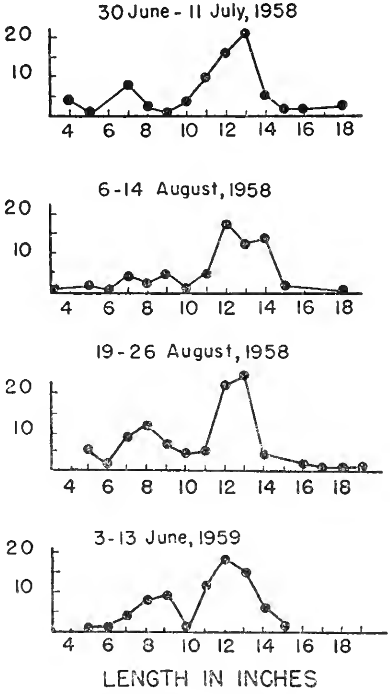

FIG. 2. Length-frequency of river carpsucker in the Neosho River, 1958 and 1959.

Young-of-the-year were taken at every station. Extensive seining along a gravel bar at the lower Neosho station indicated that the young are highly selective for quiet, shallow water with mud bottom. In these areas, young-of-the-year carpsucker were often the most abundant fish.

River carpsucker were collected more readily by use of the shocker after dark than in daylight (Table 9, p. 402).

Carpiodes velifer (Rafinesque)

High-finned Carpsucker

A specimen of *Carpiodes velifer* taken at the lower station on the Neosho in 1958 provided the only record of the species in Kansas since 1924. Many specimens, now in the University of Kansas

Museum of Natural History, were taken from the Neosho River system by personnel of the State Biological Survey prior to 1912. The species has declined greatly in abundance in the past 50 years.

Moxostoma aureolum pisolabrum Trautman

Short-headed Redhorse

The short-headed redhorse occurred at all stations. It was common at the middle and lower stations on the Neosho, rare at the upper station on the Neosho, abundant at the upper station on the Marais des Cygnes in 1957, and rare thereafter at all stations on the Marais des Cygnes. Short-headed redhorse typically occur in riffles, most commonly at the uppermost end where the water flows swiftly and is about two feet deep. An unusually large concentration was seen on 13 June, 1959, in shallow (six inches), fast water over gravel bottom at the middle station on the Neosho River.

Thirty-nine individuals were marked by clipping fins at the middle Neosho station in 1959. Four were recovered from one to 48 days later: two at the site of original capture (one 48 days after marking), one less than one-half mile downstream, and one about one mile downstream from the original site of capture.

At the middle Neosho station in 1958, this species was taken more readily by use of the shocker at night than by day (Table 9, p. 402).

Moxostoma erythrurum (Rafinesque)

Golden Redhorse

The golden redhorse was abundant at the upper Neosho station, rare at the middle Neosho station, and did not occur in collections at other stations. This species was taken most frequently over gravel- or rubble-bottoms in small pools below riffles, and was especially susceptible to collection by means of the shocker.

Twenty-nine golden redhorse of the 1957 year-class, taken at the upper Neosho station on 9 September 1958, were 6.2 to 8.6 inches in total length (average 7.4 inches); 26 individuals of the same year-class caught on 21 August 1959 were 9.3 to 13.5 inches in total length (average 10.9 inches).

Cyprinus carpio Linnaeus

Carp

The carp decreased in abundance from 1957 to 1959 at the upper and middle Marais des Cygnes station and at the middle and lower Neosho stations. Carp were more abundant in the Marais des

Cygnes than in the Neosho, although the largest number in any single collection was found in one pool at the upper Neosho station in 1958.

Carp were taken most commonly in quiet water near brush or other cover. At the middle Neosho station, collecting was most effective between the hours of 6:30 a.m. and 12:30 p.m. and least effective between 12:30 p.m. and 6:30 p.m. (Table 9, p. 402). Ripe males were taken as early as 19 April (16.1 inches, 19.4 inches T. L.) and as late as 30 July (16 inches T. L.) at the middle Neosho station. Ripe females were taken as early as 19 April at the middle Neosho station (19.2 inches T. L.) and as late as 7 July at the lower Neosho station (16 inches T. L.). Young-of-the-year were taken first at the middle Marais des Cygnes on 8 July 1957. They were recorded on later dates at the upper Marais des Cygnes and at the lower and middle Neosho stations.

Notemigonus crysoleucas (Mitchill)

Golden Shiner

The golden shiner was taken rarely at the upper Marais des Cygnes station in 1958 and 1959 and at the middle Marais des Cygnes station in 1957 and 1958. At the middle Neosho station *Notemigonus* was seined from a pond that is flooded frequently by the river, but never was taken in the mainstream.

Semotilus atromaculatus (Mitchill)

Creek Chub

The creek chub was taken only at the upper stations on both rivers. It increased in abundance at the upper Neosho station from 1957 to 1959, and was not taken in the upper Marais des Cygnes until 1959.

Hybopsis storeriana (Kirtland)

Silver Chub

A single specimen from the lower Marais des Cygnes station provides the only record of the species from the Marais des Cygnes system in Kansas, and is the only silver chub that I found in either river in 1957-1959. The species is taken often in the Kansas and Arkansas rivers.

Hybopsis x-punctata Hubbs and Crowe

Gravel Chub

The gravel chub, present only at the lower and middle Neosho stations, occupied moderate currents over clean (free of silt) gravel bottom. The gravel chub was not taken in 1957, was rare at both Neosho stations in 1958, became common at the lower Neosho station in part of 1959, but was never numerous at the middle Neosho station. Dr. F. B. Cross recorded the species as "rare" in 1952 at a collection site near my middle Neosho station, but larger numbers were taken then than in any of my collections at that station. The population was probably reduced by drought, and recovery was comparatively slow following restoration of flow.

Young-of-the-year and adults were common in collections from riffles at the lower Neosho station from 1 July through 8 July, 1959. I obtained only one specimen in intensive collections in the same area on 25, 26, and 27 August. Seemingly the species had moved off shallow riffles into areas not sampled effectively by seining.

Phenacobius mirabilis (Girard)

Sucker-mouthed Minnow

The sucker-mouthed minnow was common at the middle Marais des Cygnes station but was not taken at the upper and lower stations until 1959, when it was rare. At the middle and lower Neosho stations this fish increased in abundance from 1957 to 1959; at the upper station, sucker-mouthed minnows were not taken until 1959 when collections were made on the White farm. There, the species was common immediately below a low-head dam, but was not taken in extensive collections on the Bosch Farm in 1959.

The species was most common immediately below riffles, or in other areas having clean gravel bottom in the current. On 5 June, 1959, many individuals were taken at night (11:30 p.m.) on a shallow gravel riffle (four inches in depth) where none had been found in a collection at 5:00 p.m. on the same date.

Young-of-the-year were taken at the lower Neosho station on 24 June, 1959, and commonly thereafter in the summer.

Notropis rubellus (Agassiz)

Rosy-faced Shiner

In 1958, the rosy-faced shiner was taken rarely at the lower stations on both streams. This species is common in smaller streams tributary to the lower portions of the two rivers, and probably occurs in the mainstream only as "overflow" from tributaries. Possibly, during drought, rosy-faced shiners found suitable habitat in the mainstream of Neosho and Marais des Cygnes rivers, but reoccupied tributary streams as their flow increased with favorable precipitation, leaving diminishing populations in the mainstream.

Notropis umbratilis (Girard)

Red-finned Shiner

The red-finned shiner, most abundant at the upper Neosho station, occurred at all stations except the upper Marais des Cygnes. This fish seems to prefer small streams, not highly turbid, having clean, hard bottoms. It is a pool-dwelling, pelagic species.

Notropis camurus (Jordan and Meek)

Blunt-faced Shiner

The blunt-faced shiner was taken only in 1957, at the middle Neosho station, where it was rare. This species, abundant in clear streams tributary to the Neosho River (field data, State Biological Survey) may have used the mainstream as a refugium during drought. The few specimens obtained in 1957 possibly represent a relict population that remained in the mainstream after flow in tributaries was restored by increased rainfall.

Notropis lutrensis (Baird and Girard)

Red Shiner

The red shiner, abundant in 1952 (early stage of drought), was consistently the most abundant fish in my collections in the Marais des Cygnes and at the lower and middle Neosho stations. However, the abundance declined from 1957 to 1959 at the two Neosho stations. At the upper Neosho station the species was fourth in abundance in 1957, and third in 1958 and 1959 (Table 12).

The red shiner is pelagic in habit and occurs primarily in pools, though it frequently inhabits adjacent riffles. Collections by seining along a gravel bar at the lower station showed this fish to be most abundant in shallow, quiet water over mud bottom, or at the head of a gravel bar in relatively quiet water. At the lower end of the gravel bar in water one to four feet deep, with a shallow layer of silt over gravel bottom and a slight eddy-current, red shiners were replaced by ghost shiners or river carpsucker young-of-the-year as the dominant fish.

Fifty-nine dyed individuals were released in an eddy at the lower end of a gravel bar at the middle Neosho station on 5 June, 1959. Some of these fish still were present in this area when a collection was made 30 hours later. No colored fish were taken in collections from quiet water at the upper end of the gravel bar. A swift riffle intervening between the latter area and the area of release may have impeded their movement. Forty-six individuals, released at the head of the same gravel bar on 10 June, 1959, immediately swam slowly upstream through quiet water and were soon joined by other minnows. These fish did not form a well-organized school, but moved about independently, with individuals or groups variously dropping out or rejoining the aggregation until all colored fish disappeared about 50 feet upstream from the point of release.

Evidence of inshore movement at night was obtained on 8 June, 1959, in a shallow backwater, having gravel bottom, at the head of a gravel bar at the middle Neosho station. A collection made in the afternoon contained no red shiners, but they were abundant in the same area after dark.

In Kansas, red shiners breed in May, June, and July. Minckley (1959:421-422) described behavior that apparently was associated with spawning. Because of its abundance, the red shiner is one of the most important forage fishes in Kansas streams, and frequently is used as a bait minnow.

Notropis volucellus (Cope)

Mimic Shiner

The mimic shiner was taken only rarely at the two lower Neosho stations. This species, like *N. camurus*, is normally more common in clear tributaries than in the Neosho River, and probably frequents the mainstream only during drought.

Notropis buchanani Meek

Ghost Shiner

Field records of the State Biological Survey indicate that the ghost shiner was common in the mainstream of the lower Neosho River during drought. In 1957, the species was abundant at the lower and middle stations on the Neosho River and at the lower Marais des Cygnes station.

Collections at all stations show that the species has a definite preference for eddies—relatively quiet water, but adjacent to the strong current of the mainstream rather than in backwater remote from the channel. The bottom-type over which the ghost shiner was found varied from mud to gravel or rubble.

Notropis stramineus (Cope)

Sand Shiner

The sand shiner was taken rarely in the Neosho and commonly in the Marais des Cygnes in 1952. In my study the species occurred at all stations, but not until 1959 at the upper and lower Neosho stations. Sand shiners were found with equal frequency in pools and riffles. Spawning takes place in June and July.

Pimephales tenellus tenellus (Girard)

Mountain Minnow

The mountain minnow was common at the lower and middle Neosho stations throughout the period of study, and increased in abundance from 1957 to 1959. It was taken only in 1959 at the upper Neosho station, where it was rare. This species does not occur in the Marais des Cygnes River. The largest numbers were found in 1959 at the lower Neosho station, where this fish occurred most commonly in moderate current over clean gravel bottom. The mountain minnow, like *Hybopsis x-punctata,* was common in late June and early July but few were found in late August, 1959. The near-absence of this species in collections made in late August is responsible for the apparent slight decline in abundance from 1957 to 1959, as shown in Table 11. Metcalf (1959) found mountain minnows most commonly in streams of intermediate size in Chautauqua, Cowley and Elk counties, Kansas. The predilection of this species for permanent waters resulted in an increase in abundance during my study. With continued flow, this species possibly will decrease in abundance in the lower mainstream of the Neosho River. I suspect that the species is, or will be (with continued stream-flow), abundant in tributaries of intermediate size in the Neosho River Basin.

Pimephales vigilax perspicuus (Girard)

Parrot Minnow

The parrot minnow was not taken in the Marais des Cygnes River and was absent at the upper Neosho station until 1959. This species was common at the lower and middle Neosho stations throughout the period of study and increased in abundance from 1957 to 1959.

At the lower Neosho station, this fish preferred slow eddy-current over silt bottom, along the downstream portion of a gravel bar. The parrot minnow was taken less abundantly in the latter part of the summer, 1959, than in early summer, but the decline was less than occurred in the moutain minnow.

Pimephales notatus (Rafinesque)

Blunt-nosed Minnow

The blunt-nosed minnow was common, and increased in abundance in both rivers from 1957 to 1959. The largest numbers were found at the upper Neosho station in 1959, and a large population also was present at the lower Neosho station in 1959.

Pools having rubble bottom, bedrock, and small areas of mud were preferred at the upper Neosho station. At the lower Neosho station the fish was most common in quiet water at the lower end of a gravel bar. The parrot minnow also was common in this general area; nevertheless, these two species were seldom numerous in the same seine-haul, indicating segregation of the two. The blunt-nosed minnow was taken frequently in moderate current over clean gravel bottom, especially in late summer, 1959, when *P. notatus* increased in abundance as the mountain minnow decreased.

Pimephales promelas Rafinesque

Fat-headed Minnow

The fat-headed minnow was taken at all stations except at the lower one on the Marais des Cygnes, and was most abundant at the upper Neosho station. Intensive seining at the lower Neosho station indicated that this species preferred quiet water and firm mud bottom.

In the Neosho River in 1957 to 1959, habitats of the species of *Pimephales* seemed to be as follows: *Pimephales tenellus* (mountain minnow) occurred primarily in moderately flowing gravel riffles in the downstream portions of the river. *Pimephales vigilax* (parrot minnow) was mostly in the quiet areas having mud bottom at the downstream end of gravel bars, and less commonly on adjacent riffles, at the lower station. *Pimephales notatus* (blunt-nosed minnow) had a wider range of habitats, occurring in quiet areas and moderate currents both upstream and downstream. *Pimephales promelas* (fat-headed minnow) occurred throughout both rivers but was most abundant in the quiet water at the uppermost stations.

Campostoma anomalum (Rafinesque)

Stoneroller

The stoneroller was most abundant at the upper Neosho station and was not taken at the lower Marais des Cygnes station. This fish increased in abundance from 1957 to 1959, but was never common at the middle Marais des Cygnes or the middle and lower Neosho stations.

The stoneroller prefers fast, relatively clear water over rubble or gravel-bottom.

Ictalurus punctatus (Rafinesque)

Channel Catfish

The abundance of channel catfish was greatly reduced as a result of the drought of 1952-1956. With the resumption of normal streamflow in 1957, the small numbers of adult channel catfish present in the stream produced unusually large numbers of young. These young of the 1957 year-class, which reached an average size of about nine inches by September 1959, will provide an abundant adult population for several years.

The reduction in number of channel catfish in streams can be related to the changed environment in the drought. When stream levels were low in 1953 (Tables 1-4), fish-populations were crowded into a greatly reduced area. An example of these crowded conditions was observed by Roy Schoonover, Biologist of the Kansas Forestry, Fish and Game Commission, in October, 1953, when he was called to rescue fish near Iola, Kansas. The Neosho River had ceased to flow and a pool (less than one acre) below the city overflow dam was pumped dry. Schoonover (personal communication) estimated that 40,000 fish of all kinds were present in the pool. About 30,000 of these were channel catfish, two inches to 14 inches long, with a few larger ones. Fish were removed in the belief that sustained intermittency in the winter of 1953-1954 would result in severe winterkill. These conditions almost certainly were prevalent throughout the basin.

In addition to winterkill, crowding probably resulted in a reduced rate of reproduction by channel catfish, and by other species as well. This kind of density-dependent reduction of fecundity is known for many species of animals (Lack, 1954, ch. 7). In fish, it is probably expressed by complete failure of many individuals to spawn, coupled with scant survival of young produced by the adults that do spawn. Reproductive failure of channel catfish in farm ponds, especially in clear ponds, is well known, and is often attributed to a paucity of suitable nest-sites (Marzolf, 1957:22; Davis, 1959:10).

In the Neosho and Marais des Cygnes rivers, the intermittent conditions prevalent in the drought resulted in reduced turbidity in the remaining pools. Many spawning sites normally used by channel catfish were exposed, and others were rendered unsuitable because of the increased clarity of the water. In addition, predation on young channel catfish is increased in clear water (Marzolf; Davis, *loc. cit.*), and would of course be especially pronounced in crowded conditions. The population was thereby reduced to correspond to the carrying capacity of each pool in the stream bed.

The return of normal flow in 1957 left large areas unoccupied by fish and the processes described above were reversed. The expanded habitat favored spawning by nearly the entire adult population, and conditions for survival of young were excellent. As a result, a large hatch occurred in the summer of 1957. (Several hundred small channel catfish were sometimes taken by use of the shocker a short distance upstream from a 25-foot seine, set in a riffle). Subsequent survival of the 1957 year-class has been good. By 1959, few of the catfish spawned in 1957 had grown large enough to contribute to the sport fishery, but they are expected to do so in 1960 and 1961.

The 1957 year-class was probably the first strong year-class of channel catfish since 1952. Davis (1959:15) found that channel catfish in Kansas seldom live longer than seven years. The 1952 year-class reached age seven in 1959. The extreme environmental conditions to which these fish were subjected in drought caused a higher mortality than would occur in normal times. The adult population in the two rivers probably was progressively reduced throughout the drought, and the reduction will continue until the strong 1957 year-class replenishes it. For these reasons, fishing success was poor in 1957-1959.

Juvenile channel catfish were more abundant in the Neosho than in the Marais des Cygnes in 1958 and 1959, although both streams supported sizable populations. In the Marais des Cygnes the upper station had fewer channel catfish than the middle and lower stations. In the Neosho, populations were equally abundant both upstream and downstream. The habitat of channel catfish in streams has been discussed by Bailey and Harrison (1948).

I found adults in various habitats throughout the stream, but most abundantly in moderately fast water at the lower and middle Neosho stations. At the upper Neosho station where riffles are shallow, yearlings and two-year-olds were numerous in many of the small pools over rubble-gravel bottom. Cover was utilized where present, but large numbers were taken in pools devoid of cover. Young-of-the-year were nearly always taken from rubble- or gravel-riffles having moderate to fast current at both upstream and downstream stations.

Collections showed that young of 1957 were abundant on riffles throughout the summer and until 17 November, 1957. Subsequent collections were not made until 11 May, 1958, at which time 1957-class fish still were abundant on riffles at the lower Neosho station; on that date, the larger individuals were in deeper parts of the riffles than were smaller representatives of the same year-class.

In a later collection (2 June, 1958), numbers present on the riffles were greatly reduced and the larger individuals were almost entirely missing. Some of the smaller individuals were still present in the shallower riffle areas. Table 7 compares sizes of the individuals obtained on 2 June with sizes collected from deep riffles at the middle Neosho station on 7 June, 1958. The larger size of the group present in deep riffles is readily apparent. The yearlings almost completely disappeared from subsequent collections on riffles.

A bimodal size-distribution of young-of-the-year was noted also in 1958 and 1959; but, no segregation of the two sizes occurred on riffles in summer. Marzolf (1957:25) recorded two peaks in spawning activity in Missouri ponds. Two spawning periods may account for the bimodal size distribution of young-of-the-year observed in my study.

In 1959, young-of-the-year began to appear in the latter part of June and became abundant by the first part of July. Individuals as small as one inch T. L. were taken in gravel-bottomed riffles on 1 July, 1959.

Yearling individuals at the lower and middle Neosho stations showed a pronounced tendency to move into shallow, moderately fast water over rubble or gravel bottom at night, where they were nearly ten times more abundant than in daytime (Table 9). Adults probably have the same pattern of daily movement as yearlings, except that at night the adults move to deeper riffles. Bailey and Harrison (1948:135-136) demonstrated that channel catfish feed most actively from sundown to midnight.

Channel catfish (especially two-year-olds and adults) were abundant on a rubble-riffle during the day in some collections at the lower Neosho station in 1959.

TABLE 7. LENGTH-FREQUENCY OF CHANNEL CATFISH FROM THE NEOSHO RIVER, 1957, 1958 AND 1959. (NUMBERS IN VERTICAL COLUMNS INDICATE THE NUMBER OF INDIVIDUALS OF A CERTAIN SIZE COLLECTED ON THAT DATE.)

Length in inches	Nov. 2 1957	June 2 1958 (shallow riffle)	June 7 1958 (deep riffle)	Sept. 9 1958	Sept. 11 1959
1.5				1	
2.0	3				
2.5	13	2		1	2
3.0	4	11		3	4
3.5	3	21	7	1	14
4.0		11	12		9
4.5		4	10	1	
5.0		2	11	2	
5.5		1	7	26	
6.0				58	2
6.5			1	32	5
7.0				16	5
7.5			1	4	5
8.0					22
8.5					45
9.0					81
9.5					41
10.0					21
10.5					8
11.0					4
11.5					1
12.0					3
12.5					1
13.0					1

Near the end of the spawning season in 1959, I found spawning catfish at the lower Neosho station. Ripe females were taken between 9 June and 30 June, 1959; and, on 19 June I found a channel catfish nest with eggs (water temp. 79° F.). The nest-site was a hole in the base of a clay bank; the floor was clean gravel with a small mound of gravel at the entrance. The nest-opening, five to six inches in diameter, widened almost immediately into a chamber about two and one-half feet long and one foot wide. Normally the water was about six inches deep in the mainstream as it ran over a riffle adjacent to the catfish nest. When I put my hand into the opening the fish bit vigorously, but became quiescent when I stroked its belly. I then felt the rounded gelatinous mass of eggs on the bottom of the nest. On June 22 (water temp. 86° F.) the fish was removed, struggling, from the nest, and returned to the stream. The next day (23 June 1959, water temp. 84° F.) the eggs had hatched and the young were in a swarm in the nest. The adult did not attempt to bite but left as soon as I put my hand into the hole.

Marzolf (1957:25) reports that young remain in the nest from seven to eight days after hatching. My seining records show a marked increase in abundance of small young-of-the-year on the first of July. Probably the time of hatching of the nest described above correlated well with hatches of other nests.

One and sometimes two channel catfish were found in other holes in the stream-bank or bottom. The fish occasionally attacked my hand vigorously, but at other times remained quiet or left without attacking. No other channel catfish eggs were found, although one hole under a rock in the middle of the river had one or two individuals in it each time it was checked until 11 July, 1959. A local fisherman informed me of his belief that these holes are occupied only in the spawning season.

Observations that I made in a pond owned by Dr. E. C. Bryan of Erie indicated that channel catfish, when disturbed in the early stages of guarding the eggs, either eat the eggs and abandon the nest or leave the nest exposed to predation by other animals. In the later stages of nesting, the fish, if removed, will return to guard the nest. After the eggs hatch the guarding response probably diminishes and the fish leaves the nest readily.

At the lower Neosho station, several "artificial" holes were dug into the clay bank and two pieces of six-inch pipe were forced into the bank. Nearly all these holes were occupied by catfish for a short period in June; many of the holes were enlarged, either by the current or by fish. I suspect that fish enlarged some holes, because in the spawning season several males were observed that had large abrasions atop their heads, around their lips, and to a lesser extent on their sides. These could have been caused by butting and scraping the sides, roof and floor of a hole. I found it possible to enlarge the holes by rapidly moving my hand while it was inside a hole.

The growth-rate of channel catfish in the Neosho was approximately the same at all stations, and the large 1957 year-class grew to an average size of about nine inches by mid-September, 1959 (Table 7). Channel catfish mature at a total length of 12 to 15 inches. Thus, most individuals of the 1957 year-class in the Neosho River probably will mature in their fourth or fifth summer (1960 or 1961 spawning season).

The sizes attained by young-of-the-year in 1957 differed in the two rivers. Six hundred and thirty-three young taken in the Marais des Cygnes River attained an average size of 4.7 inches (range two to six inches) by mid-September. (Age was determined by length-frequency and verified by examining cross-sections of fin-spines from the larger individuals). One hundred and fifty young from the Neosho River averaged 3.0 inches (range 2 to 3.7 inches) on 2 November. Gross examination of the riffle-insect faunas indicated a larger standing crop in the Neosho than in the Marais des Cygnes River. Thus, the slower growth of young channel catfish in the Neosho seemed not to be correlated with food supply. Bailey and Harrison (1948:125-130) found that young channel catfish in the Des Moines River, Iowa, fed almost exclusively on aquatic insect larvae. My observations indicate that this is true in the Neosho and Marais des Cygnes rivers also.

Young produced in 1958 in the Neosho River attained an average total length of three inches by 26 August, and young produced in 1959 attained an average size of 3.5 inches by 11 September. Both groups probably continued growth until October, and may have averaged four inches total length at that time.

The 1958 and 1959 year-classes were much less abundant than were the 1957 young. Therefore, it seems likely that the growth of the 1957 young in the Neosho River was depressed because of crowding. The 1959 year-class was larger than the small 1958 year-class, thus conforming to a general expectation that strong year-classes will be followed by weak year-classes.

Reproduction by channel catfish in 1957 seemed greater in the Neosho River than in the Marais des Cygnes River (Table 10); this coincided with a greater change in volume of flow in the Neosho River than in the Marais des Cygnes River (Tables 1-4). The 1957 year-class seemed more crowded, and grew more slowly, in the Neosho than in the Marais des Cygnes River.

Ictalurus natalis (LeSueur)

Yellow Bullhead

Yellow bullhead were taken only at the middle station on the Marais des Cygnes and upper station on the Neosho. The yellow bullhead is more restricted to streams than is the black bullhead. Both species decreased in abundance during a period of continuous flow (1957 to 1959) following drought at the upper Neosho station. Collections in 1958-'59 indicated an increase in average size. Of four individuals marked and released at the upper Neosho station in 1959, one was recaptured about three hours after being released. It had not moved from the area of release.

Ictalurus melas (Rafinesque)

Black Bullhead

The black bullhead was abundant at the upper stations on each river, especially in backwaters having mud-bottom. The species was not taken in the mainstream of the lower and middle Neosho stations, but was taken at the middle Neosho station in a pond that is often flooded by the river. Although the fish was common or abundant in nearly all pools at the upper Neosho station, it was most abundant in one pool that had a bottom predominately of mud.

At the middle Marais des Cygnes station, 109 individuals were collected and fin-clipped on 8, 9 and 24 July 1957. Three of the 19 marked on 8 July were recaptured in the same area on 9 July. The area was poisoned on 13 September, 1957, and 130 black bullhead were taken, none of which had been marked.

In 1959, 96 black bullhead were taken at the upper Neosho station (five in Area 1 and 91 at the White Farm). In these collections, 25 were marked (fin-clipped or dyed) and six were recaptured. Four of the six had not left the area of capture one and two days after being released. The fifth fish recaptured was one of five individuals that had been displaced one pool downstream. When recaptured seven days later, this fish had moved upstream over two steep riffles (two to three inches deep, 75 feet and 166 feet long) past the site of original capture to the next pool. The sixth fish, marked at the same time but returned to the original pool, was recaptured nine days after original capture and had moved upstream over a long riffle (two to three inches deep, 166 feet long) and a short riffle into the second pool above the original site of its capture.

Rotenone was applied to a small (.04 acre-feet) backwater ditch having a soft mud bottom at the upper Marais des Cygnes station on 25 July, 1957; 1526 black bullhead, one green sunfish and one white crappie were collected. A sample of 60 bullhead averaged 4.6 inches T. L. (range 3.5 to 6.6 inches) and 540 individuals averaged .7 ounce each. These fish probably represented the 1956 year-class.

The upper Neosho station had a large population of black bullhead, strongly dominated by fish less than four inches T. L. (range 1.5 to 3.8 inches), in the spring of 1957. Most were approximately two inches T. L. and probably represented the 1956 year-class. Growth, according to length-frequency, following restoration of stream-flow, shows a regular increase in length of this dominant 1956 year-class (Fig. 3). A scarcity of young, especially in 1958 and 1959, is apparent in Fig. 3. This may be due to the fact that a strong year-class usually is followed by one or several weak year-classes. However, it more probably reflects the fact that black bullhead are characteristically pond fish, and as such are not so well adapted to reproduction in flowing streams as are many other species. Metcalf (1959) found this species most abundantly in the intermittent headwaters of Walnut River and Grouse Creek in Cowley County, Kansas.

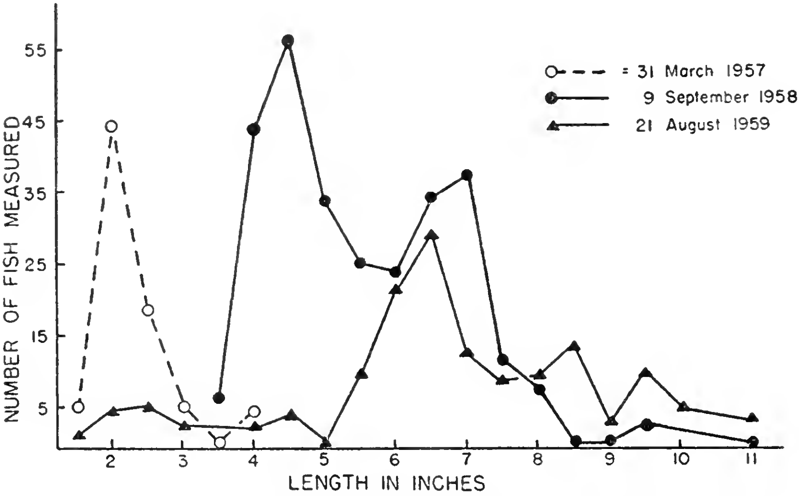

FIG. 3. Length-frequency of black bullhead at the upper Neosho station, 1957, 1958 and 1959.

Pylodictis olivaris (Rafinesque)

Flat-headed Catfish

The flathead is the largest sport-fish occurring in Kansas. Several weighing more than 40 pounds are caught from streams each year, and the species reportedly attains sizes in excess of one hundred pounds. Several aspects of the biology of the flathead in Kansas have been discussed by Minckley and Deacon (1959).

The abundance of flathead declined slightly from 1957 through 1959, counting fish of all sizes. This trend is attributable to a large hatch in 1957; the 1957 year-class strongly dominated the population throughout my study. Natural mortality in that year-class was compensated by increased average size of the individuals (to six inches in autumn, 1958, and 11 inches in autumn, 1959).

The numbers of flathead caught at the upper stations on the Neosho and Marais des Cygnes rivers differed from the general trend in that the species was rare in 1957 and increased slightly by 1959. Flathead are most numerous in large streams, and in the drought they probably were almost extirpated from the headwaters. After 1957, continuous flow and increased volume of flow were accompanied by a gradual increase in numbers of flathead in the upstream parts of the two rivers. The species was most abundant at the middle and lower Neosho stations, where 10.5 per cent of all fish shocked in 1957 and 1958 were *P. olivaris.*

The habitat of the flathead varied with size of the individuals. Young-of-the-year inhabited swift riffles having rubble bottom; individuals four to 12 inches in total length were distributed throughout the stream; those more than 12 inches in total length were most commonly in pools in association with cover (rocks, or drifts of fallen timber).

Male flathead mature at 15 to 18 inches total length, females at 18 to 20 inches. The spawning season in 1959 probably began in early June and extended to mid-July. I attempted to find spawning fish on 19 June and for one month thereafter. On 19 June nine holes were dug into a 75-yard section of a clay bank adjacent to a long, shallow, rubble riffle. A flathead was first found in one of these holes on 22 June, and others were frequently found in this and one other hole until mid-July. Although channel catfish were often found in nearby holes, that species was never present in the two holes used by flatheads. The holes occupied by flathead (as well as those used by channel catfish) characteristically had silt-free gravel bottoms and a ridge of clean gravel across the entrance.

A nest containing a flathead and eggs was located on 11 July. In checking the hole I first put by foot into the entrance, then slowly advanced my hand into the hole, feeling along the bottom with my fingers until they entered the open mouth of a large catfish. I backed off slowly and then felt beneath the fish. The fish was directly above the egg-mass, seemingly touching the eggs with its belly. As I touched the front of the egg-mass the fish struck viciously, taking my entire fist into its mouth. It continued striking until I removed my hand from the hole after obtaining a small sample of eggs, which proved to be in an early stage of development (no vascularization evident).

When the nest was checked again on 13 July the eggs and fish were gone. As in the case of channel catfish, I suspect that disturbance of a flathead in the early stages of guarding the nest results in destruction of the nest either by the guardian fish or by predation resulting from its absence.

The hole occupied by the above fish was one that I had dug seven to nine inches in diameter and extending two and one-half to three feet into the bank. At the time this fish occupied the hole its depth was approximately the same as originally, but the entrance had been enlarged to 14 inches in diameter, and the chamber widened to 32 inches. The holes were checked later in the summer and all were heavily silted or had been undercut by action of the current.

The number of flathead of catchable size was not reduced as severely during my study as was the number of large channel catfish. Flathead have a longer life-span than channel catfish; therefore, it is not surprising that, of flathead and channel catfish that survived the drought, a higher proportion of flathead persisted throughout the next three years, in which my study was made. In drought, when fish were concentrated in residual pools, the piscivorous (fish eating) habit of flatheads may have favored their survival.

The growth rate of flathead taken from the Neosho River in 1957 and 1958 was reported by Minckley and Deacon (1959:351-352). Individuals hatched in 1955 and 1956 and collected in 1957 had attained average sizes of 9.5 inches and 4.8 inches, respectively, by the end of the 1956 growing-season.

Flatheads of the 1956 and 1957 year-classes attained average sizes of 8.7 and 3.2 inches, respectively, by the end of the 1957 growing season. These data indicate that growth was retarded in the summer of 1957. Many species, including *P. olivaris,* had an exceptionally large hatch in 1957, associated with increased water levels in that year. Despite the great increase in amount of water, I suppose that young-of-the-year and yearlings were subjected to crowding resulting from exceptional hatches. This caused reduction in growth of young flathead, and probably in several other species.

Food of flatheads 4.0 inches and shorter was nearly all insect larvae; that of fish 4.1 to 10 inches was insect larvae, fishes and crayfish; and that of larger flatheads was mostly fish and crayfish.

The specific kind of food eaten was correlated with abundance of the food item in the stream (Minckley and Deacon, 1959:350-351).

Noturus flavus Rafinesque

Stonecat

The stonecat was not taken at the upper Marais des Cygnes station, and was less abundant at the middle Marais des Cygnes station than at other stations. The abundance of the stonecat was greatest at the lower Marais des Cygnes station in 1957 and at the upper Neosho station in 1959. The species increased in abundance from 1957 to 1959 in the Neosho River, where the principal habitat was riffles over rubble bottom.

Thirty-three stonecats were marked at the upper Neosho station in 1959. Five of these were recaptured three hours after release, all near the point of release. One individual was taken from a riffle, fin-clipped, and released at the foot of the next riffle downstream. When recaptured four days later, this fish was still in the area of release. Young-of-the-year were taken on July 1, 1959, at the lower Neosho station.

Noturus gyrinus (Mitchill)

Tadpole Madtom

Trautman (1957:444-445) describes the habitat of the tadpole madtom as "low-gradient lowland streams, springs, marshes, oxbows, pothole lakes, and protected harbors and bays of Lake Erie, where conditions were relatively stable, the water was usually clear, the bottom was of soft muck which generally contained varying amounts of twigs, logs, and leaves, and where there usually was an abundance of such rooted aquatics as pondweeds and hornwort. The species seemed to be highly intolerant to much turbidity and rapid silting, . . ." The tadpole madtom was obtained only at the middle Marais des Cygnes station in a small, deep, mud-bottomed pool in 1957 after water levels, and probably turbidity, had been low for five years. The occurrence provides the westernmost record station in Kansas. Cross and Minckley (1958:106) reported the species from the lower part of the Marais des Cygnes in Kansas.

Noturus nocturnus Jordan and Gilbert

Freckled Madtom

The freckled madtom was taken only at the middle Neosho station on 19 April, 1958. This species occurs most frequently in small streams, and individuals living in the mainstream of the Neosho probably are "strays" from nearby tributaries. This species may have utilized the mainstream as a refugium in the drought of 1952-'56.

Noturus exilis Nelson

Slender Madtom

The slender madtom was taken only at the middle Marais des Cygnes station in the fall of 1957. This species prefers permanent riffles of clear streams (Deacon and Metcalf, 1961:317). My specimen possibly strayed from a nearby tributary; or, it was a relict from a population living in the mainstream during drought.

Noturus sp.

Neosho Madtom

A description of this species, which is endemic to Neosho River, has been prepared but not yet published by Dr. W. Ralph Taylor. I found the Neosho madtom only at the middle station in 1958 and 1959, and at the lower station in 1959, where the species was common in shallow water having moderate current over clean gravel bottom. Specimens were most effectively collected by digging into the gravel above the seine and allowing the gravel to wash into the seine. In 1952, Cross (1954:311) found this species in abundance in riffles at the confluence of the South Fork and Cottonwood River, and at several other localities in the Neosho mainstream (personal communication). The Neosho madtom is nearly restricted to gravel riffles having moderate flow; therefore, it may be drastically reduced by intermittency of flow. I found none in 1957 and few in 1958. By 1959, the third summer of continuous flow, the Neosho madtom was again common.

Fundulus notatus (Rafinesque)

Black-striped Topminnow

The black-striped topminnow was rare in the mainstream at the lower Marais des Cygnes and the middle and lower Neosho stations, where it was found in quiet water near shore.

Near the middle Neosho station, a large population was present in an oxbow lake that is frequently flooded by the river.

Labidesthes sicculus (Cope)

Brook Silversides

The brook silversides occurred rarely at the lower Marais des Cygnes and at the middle and lower Neosho stations.

Micropterus dolomieui Lacépède

Small-mouthed Bass

One individual was taken at the lower Neosho station in 1957.

Micropterus punctulatus punctulatus (Rafinesque)

Spotted Bass

The spotted bass occurs in Kansas only in the southeastern part of the state—in southern tributaries of the Osage system, in Spring River drainage, and in relatively clear streams of the Flint Hills. At my stations on the Neosho River, this fish was more abundant in 1957 than in 1958 or 1959.

Spotted bass were taken most frequently over rubble bottom or near boulders in moderate current. Collections made in the evening or early morning more often contained spotted bass than collections made at other times of day (Table 9). Data from a few specimens that were marked, released, and recaptured indicated that the species is relatively sedentary; therefore, the greater abundance in the morning and evening collections probably indicates increased activity during these periods, possibly in connection with feeding. The spawning season in 1957 may have continued as late as 10 July when a ripe female 11.3 inches T. L. was taken. Young-of-the-year were taken on 24 June in moderate current over gravel bottom and in quiet water over mud bottom.

Spotted bass normally form a small part of the game-fish fauna in the lower Neosho River. The species attains greater abundance in smaller, clear streams of the Arkansas River Basin in Kansas (Cross, 1954, and unpublished data of State Biological Survey of Kansas). During the drought, the lower Neosho probably assumed many characteristics of a smaller stream in normal times. Flow was reduced or entirely interrupted and turbidity was lessened. These conditions resulted in faunal changes in which spotted bass were more prominent than in years of normal flow. During this period of reduced flow, some fishermen turned from catfishing to bass-fishing; I think this constitutes evidence for an increase in numbers of bass, accompanied by a decrease in numbers of channel catfish. With the return of continuous flow and a consequent rise in turbidity, bass declined in abundance in the mainstream.

Micropterus salmoides salmoides (Lacépède)

Large-mouthed Bass

The large-mouth was rare at all stations. It prefers quiet water near cover; to become abundant, the large-mouth probably requires clearer water than is afforded by most Kansas streams. This species, like spotted bass, declined in abundance during the period of study. Nevertheless, young-of-the-year were taken in 1957 and 1958 (earliest date of capture, 7 June in 1958).

Lepomis cyanellus Rafinesque

Green Sunfish

Green sunfish were taken at all stations, but most abundantly at the upper Neosho station where the number captured increased slightly from 1957 to 1959. Young-of-the-year and adults were most common in shallow backwater. At the upper Neosho station green sunfish inhabit quiet pools, where recaptures of marked fish indicated that the species is notably sedentary in habit. Hasler and Wisby (1958) have shown that green sunfish exhibit a homing reaction.

This fish provides some sport for fishermen, especially in the smaller streams, but I found few green sunfish that were larger than six inches T. L. at any station.

Lepomis megalotis (Rafinesque)

Long-eared Sunfish

Long-eared sunfish were taken at all stations but were notably more abundant in the Neosho River, where the largest population occurred at the upper station. In all three years of the study, large samples were obtained by means of rotenone in the same pool at the upper Neosho station. There were fewer long-eared sunfish present each year, and average size increased slightly. Collections in other pools at this station indicated that long-eared sunfish maintained a high level of abundance throughout my study.

Long-eared sunfish occurred in pools having bottoms of gravel or bedrock at the upper Neosho station, or near shore over rubble or gravel in slow to moderate current at the middle Neosho station.

Lepomis humilis (Girard)

Orange-spotted Sunfish

The orange-spotted sunfish occurred at all stations; it was most abundant in the Neosho River, especially at the uppermost station. This fish was taken in a variety of habitats, but was most common in areas where the current was slack, often over mud or silt bottom.

Lepomis macrochirus Rafinesque
Bluegill

Bluegill were taken at all stations but were rare. This species occurred exclusively in pools, usually near cover (brush or trees in the water). Bluegill are predominately pond-fish in Kansas, and populations in rivers may consist partly of individuals that escaped from ponds in time of overflow. I know of no stream in Kansas that has a population large enough to contribute significantly to the sport fishery.

Pomoxis nigromaculatus (LeSueur)
Black Crappie

This species was represented by only one specimen, taken at the lower Neosho station in 1957.

Pomoxis annularis Rafinesque
White Crappie

White crappie were taken at all stations, but were common only at the upper and middle stations on the Marais des Cygnes and the upper Neosho station. At the last station, this fish was abundant in a single large pool that contained much more water during drought than any other area at this station. There was little dispersal into several smaller pools, below the large pool, which were sampled in 1957, 1958 and 1959. White crappie were not taken in the lower pools until 1959, and then were rare. Most crappie were taken in quiet water near cover or near shore.

Young-of-the-year were found in 1957, 1958 and 1959, but never abundantly. At the lower Neosho station in 1959, ripe individuals were collected on 19 June, a spent female on 24 June, and young-of-the-year on 1 July. The young were present in quiet, shallow water over mud bottom at the lower end of a gravel bar. Large white crappie (10-14 inches T. L.) were common at the middle and lower Neosho stations in 1957 and in April, 1958. Large fish were almost entirely absent from later collections. Average size, maximum size and abundance declined during the period of study.

Percina phoxocephala (Nelson)
Slender-headed Darter

The slender-headed darter was taken at all stations but was more abundant in the Neosho than in the Marais des Cygnes. The lower Marais des Cygnes, however, was the only station with a relatively large population in 1957. Slender-headed darters were rare in the Neosho River in 1957 and did not become common until 1959.

The largest population was found at the upper Neosho station in 1959. This darter occurs most frequently in swift water over gravel bottom, but was taken in various habitats, including an intermittent pool at the upper Neosho station on 7 September, 1957.

At the middle and lower Neosho stations, considerably greater numbers were taken in June, July, and early August than in May or late August. The abundance in my collections diminished from a peak in early July, to scarcity in late August.

Young-of-the-year were taken at the lower Neosho station on 1 July, 1959 (and subsequently), in moderately fast water over gravel. On 21 August, 1958, a ripe female (eggs stripped easily) was the only slender-headed darter present in a collection from riffles at the middle Neosho station.

Percina caprodes (Rafinesque)

Logperch

Logperch were not taken in the Marais des Cygnes. They were rare in the Neosho, where they were taken most frequently at the upper station in water two to three feet deep, over gravel bottom, in moderate to slight current. This species was present in intermittent pools at the upper Neosho station in 1957.

Percina copelandi (Jordan)

Channel Darter

One specimen was taken at the lower Neosho station in 1959. Because no others ever have been found in the mainstream of the Neosho River, I suspect that my specimen is a "stray" from one of the smaller tributaries, where channel darters are locally common.

Etheostoma flabellare Rafinesque

Fan-tailed Darter

The fan-tailed darter is represented in my collections by one specimen, obtained in the mainstream of the Neosho River at the lower station in 1957. Records of this species in Kansas are almost confined to the smallest, clear, permanent streams of the southeastern part of the state. My specimen may represent a small population that retreated to the mainstream of the Neosho during drought.

Etheostoma spectabile (Agassiz)

Orange-throated Darter

Orange-throated darters were common at the upper Marais des Cygnes and upper Neosho stations in 1959, rare at the middle and lower Neosho stations, and absent from the middle and lower Marais des Cygnes stations. The species was found almost exclusively on upstream riffles over gravel-rubble bottom. The population in the upper Neosho was decimated by drought, and the fish did not become common until the summer of 1959, the third year after resumption of normal stream-flow.

Deacon and Metcalf (1961:320) indicated that long periods of intermittency result in depletion or elimination of populations of the orange-throated darter in the Wakarusa River, Kansas. A limited number of orange-throated darters probably survived in the few permanent pools in the upper Neosho and provided the brood-stock necessary to repopulate this section of the stream.

Aplodinotus grunniens Rafinesque

Freshwater Drum

Drum were taken at all stations, but were most abundant at the middle and lower Neosho stations. A high level of abundance also was found in 1957 at the middle Marais des Cygnes station. The abundance of drum declined from 1957 to 1959, but the average size increased because of a dominant 1957 year-class that was moderately reduced by natural mortality in 1958-'59. Although the population was composed largely of young-of-the-year and adults in 1957, it was dominated by yearling individuals in 1958. By 1959 the number had declined considerably and the population consisted mostly of juveniles and adults. Fish of the 1957 year-class reached a length of approximately ten inches by mid-summer of 1959 (Table 8).

Adults were taken in a variety of habitats, but most often in quiet water. On the other hand, yearlings were extremely abundant in 1958 near shore in shallow, moderately fast water over rubble bottom at night. Drum were rare in the same areas in daylight (Table 9). Young-of-the-year occur in shallow, quiet water, usually over mud-bottom.

The freshwater drum matures at about 12 inches T. L. Ripe males were taken as late as 23 June 1959; however, the height of the spawning season probably is in May.

TABLE 8. LENGTH-FREQUENCY OF FRESHWATER DRUM FROM THE MIDDLE NEOSHO STATION IN 1957, 1958 AND 1959.

Total length in inches	Aug.19 1957	Aug. 19-26 1958	July 27-Aug. 4 1959
2		1	
3	1		
4	4		
5		1	
6		12	
7		21	1
8	3	14	2
9	3	3	2
10	4	6	6
11	2	4	1
12		2	
13			2
14			1

TABLE 9. AVERAGE NUMBER OF INDIVIDUALS CAPTURED PER HOUR, USING THE SHOCKER, AT DIFFERENT TIMES OF THE DAY AND NIGHT AT THE MIDDLE NEOSHO STATION IN 1958. NUMBERS IN PARENTHESES INDICATE TOTAL NUMBER CAPTURED.

SPECIES	Morning 5 hours of effort expended 6:30 a.m. 12:30 p.m.	Afternoon 6 hours of effort expended 12:30 p.m. 6:30 p.m.	Early night 18 hours of effort expended 6:30 p.m. 12:30 a.m.	Late night 8 hours of effort expended 12:30 a.m. 6:30 a.m.
Long-nosed Gar	0	0.3 (2)	1.2 (21)	1.1 (9)
Short-nosed Gar	0.2 (1)	0	0.2 (3)	0.4 (3)
Gizzard Shad	0.2 (1)	0.3 (2)	0.1 (1)	0.1 (1)
Black Buffalo	0	0.2 (1)	0.1 (1)	0
Small-mouthed Buffalo	0.4 (2)	0.3 (2)	0.8 (14)	0.8 (6)
River Carpsucker	3.4 (17)	3.3 (20)	5.7 (102)	4.9 (39)
Redhorse	0	0.2 (1)	0.6 (10)	0.6 (5)
Carp	1.8 (9)	0.2 (1)	0.7 (12)	0.8 (6)
Channel Catfish	1.6 (8)	1.0 (6)	10.2 (183)	10.5 (84)
Flathead	2.2 (11)	1.3 (8)	2.4 (43)	3.6 (29)
Spotted Bass	0.4 (2)	0.5 (3)	0.3 (6)	0.1 (1)
Green Sunfish	0.2 (1)	0.2 (1)	0.2 (3)	0.1 (1)
Long-eared Sunfish	0	0	0.1 (2)	0.4 (3)
Orange-spotted Sunfish	0.2 (1)	0	0	0
White Crappie	0.2 (1)	0.2 (1)	0.2 (5)	0.4 (3)
Freshwater Drum	1.0 (5)	0.8 (5)	5.6 (101)	5.3 (42)
Number captured per hour	13.4	9.3	29.5	33.8

TABLE 10. NUMBERS OF FISH SEEN OR CAPTURED PER HOUR BY USE OF THE SHOCKER. EXCLUDES FISH TAKEN BY SHOCKING INTO A SEINE ON RIFFLES; YOUNG-OF-THE-YEAR CHANNEL CATFISH AND FLATHEAD CATFISH PREDOMINATED IN SAMPLES TAKEN BY THAT METHOD.

SPECIES	Marais des Cygnes River							
	Upper			Middle			Lower	
	1957	1958	1959	1957	1958	1959	1957	1958
Gar	.7	1.3	1.2	.6	2.7	......	2.2	9.4
Gizzard Shad	.9	.2	......	9.9	2.5	......	......	.5
Buffalo	2.0	3.7	.6	.8	2.0	......	5.7	6.4
River Carpsucker	4.0	4.9	.6	6.5	2.2	2.0	1.8	3.9
Shortheaded Redhorse	3.3	.9	.6	.8	.2	......	......	......
Carp	10.6	6.4	2.4	8.6	5.0	3.5	6.0	10.4
Black Bullhead	......	......	......	3.9	17.2	......	......	......
Channel Catfish	.5	.9	......	4.7	2.5	......	1.8	.7
Flathead	.2	......	2.4	.5	......	......	1.8	.5
Largemouth	1.0	......	......	.3	.2	......	......	......
White Crappie	1.7	5.1	.6	1.3	.7	......	......	.2
Freshwater Drum	.9	1.6	.6	24.5	2.2	......	.7	.2
Hours shocked	4½	4½	1⅔	4	4	2	2⅚	4½

SPECIES	Neosho River					
	Middle			Lower		
	1957	1958	1959	1957	1958	1959
Gar	3.2	4.2	3.8	5.3	4.9	8.4
Gizzard Shad	.5	.2	.4	1.9	1.0	.4
Buffalo	2.9	1.8	1.2	6.2	.9	1.5
River Carpsucker	5.5	7.4	2.9	7.5	13.3	6.3
Shortheaded Redhorse	1.9	.6	1.6	.7	....	1.6
Carp	2.1	2.1	1.4	3.4	1.2	1.1
Channel Catfish	2.6	8.8	.9	107.0	.5	.7
Flathead	7.6	3.7	2.7	10.8	.2	1.2
Bass	1.6	.4	.1	.2	.2	.1
White Crappie	....	.9	.2	1.8	.7	.1
Freshwater Drum	3.9	3.3	.8	15.9	2.8	.7
Hours shocked	5⅔	55⅚	48½	4⅙	4	16⅚

TABLE 11. NUMBER OF OCCURRENCES (Roman type) AND NUMBER COUNTED (*Italic type*) PER SEINING UNIT. ONE SEINING UNIT EQUALS 30 SEINE-HAULS (ten each with the 4-foot, 12-foot and 25-foot seine) OF WHICH SIX RANDOMLY-CHOSEN HAULS WERE COUNTED. DASHES SIGNIFY THAT THE SPECIES OCCURRED IN UNCOUNTED COLLECTIONS ONLY.

SPECIES	Marais des Cygnes stations						Neosho	
	Upper		Middle		Lower		Lower station	
	1957	1959	1957	1959	1957	1959	1957	1959
Golden Shiner	......	......	—	......	......	......	......	......
Creek Chub	......	—	......	......	......	......	......	......
Silver Chub	......	......	......	......	—	......	......	......
Gravel Chub	......	......	......	......	......	......	......	3.0 *2.3*
Sucker-mouthed Minnow	—	6	......	3 *1*	......	1	2	10.0 *43.0*
Red-finned Shiner	......	......	......	1	2.5 *5.0*	2	......	4.7 *2.3*
Blunt-faced Shiner	......	......	—	......	......	......	......	......
Red Shiner	21 *6*	15	8 *4*	19 *22*	16.0 *69.0*	15 *22*	27 *1119*	20.0 *102.0*
Mimic Shiner	......	......	......	......	......	......	—	......
Ghost Shiner	7.5	1	......	1	9.5 *96.5*	2	17 *54*	11.7 *76*
Sand Shiner	—	7	......	8 *2*	1.5	3	......	1 *.3*
Mountain Minnow	......	......	......	......	......	......	12 *25*	9.3 *13.6*
Blunt-nosed Minnow	—	2	......	8	1.0 *.5*	1	6 *4*	14.0 *7.6*
Parrot Minnow	......	......	......	......	......	......	12 *6*	19.0 *28.6*
Fat-headed Minnow	10.5 *1.5*	4	5 *2*	7 *1*	......	......	......	8.3 *3.0*
Stoneroller	—	6	—	......	......	......	—	2.3 *1.0*
Black Bullhead	......	......	......	......	.5	......	......	......
Channel Catfish	4.5 *1.5*	2	1 *1*	13 *7*	5.0 *1.0*	10 *6*	12 *5*	6.3 *41.6*
Flathead	—	1	—	—	1.0	......	—	.3
Stonecat	......	......	—	......	6.0 *.5*	......	—	1.0
Neosho Madtom	......	......	......	......	......	......	......	3.3 *2.0*
Brook Silversides	......	......	......	......	.5 *1.0*	......	......	1.7
Black-striped Topminnow	......	......	......	......	1.0 *1.0*	2	......	1.0 *.7*
Spotted Bass	......	......	......	......	......	......	2	3.7 *.3*
Largemouth	......	......	1 *1*	3 *1*	......	......	1 *2*	......
Green Sunfish	9 *7.5*	8	9 *3*	17 *3*	11.0 *12.0*	3 *1*	7 *2*	10.0 *3.6*

TABLE 11. NUMBER OF OCCURRENCES (Roman type) AND NUMBER COUNTED (*Italic type*) PER SEINING UNIT. ONE SEINING UNIT EQUALS 30 SEINE-HAULS (ten each with the 4-foot, 12-foot and 25-foot seine) OF WHICH SIX RANDOMLY-CHOSEN HAULS WERE COUNTED. DASHES SIGNIFY THAT THE SPECIES OCCURRED IN UNCOUNTED COLLECTIONS ONLY—*Concluded.*

SPECIES	Marais des Cygnes stations						Neosho	
	Upper		Middle		Lower		Lower station	
	1957	1959	1957	1959	1957	1959	1957	1959
Long-eared Sunfish..	......	......	......	......	.5	......	6	4.3 *.7*
Orange-spotted Sunfish.........	4.5 *6*	—	2 *4*	3	2.5	......	12 *5*	12.0 *5.0*
Bluegill............	1.5	1	......	6 *1*	3.5	1	1	.3 *.3*
White Crappie......	......	......	4 *7*	4	......	......	......	......
Logperch..........	......	......	......	......	......	......	1	.3 *.7*
Slender-headed Darter..........	—	13	......	2	6.5 *15.0*	3 *1*	1	8.3 *3.0*
Orange-throated Darter..........	—	7	......	......	......	......	1	—
Seining units.......	$\frac{2}{3}$	1	1	1	2	1	1	3

FISH-FAUNA OF THE UPPER NEOSHO RIVER

Collections at the upper Neosho station were more intensive than at any other station, especially in 1959. Rotenone was used in the summers of 1957, 1958 and 1959, to obtain large samples of the population in one section of the stream. In September, 1959, the shocker was used in other sections in order to estimate populations in particular pools and riffles, to measure variability in the fauna between areas having slightly different habitat, and to record movement of marked individuals in a short section of the stream.

Description of Study-areas

Two sections of the stream, each about one-half mile long (See p. 366), were studied. Additional description of particular areas is presented below. Area 1 and the pools in which rotenone was used are on the Bosch Farm approximately two miles upstream from the White Farm where Areas 2, 3, 4, 5, 6 and 7 are situated.

Area 1 has a length of 210 feet, an average width of four feet, and a maximum depth of two feet. The upper half is a swift, rubble riffle four inches in average depth; the lower half is one and one-half feet in average depth and has a slow current (Pl. 29, Fig. 1).

Area 3 has a length of 186 feet, an average width of 34 feet, and a maximum depth of two and one-half feet. This area includes a shallow riffle at both upstream and downstream ends of a pool 73 feet long and approximately one foot in average depth (Pl. 29, Fig. 2).

Area 5 has a length of 250 feet, an average width of 50 feet, and a maximum depth of two and one-half feet. This is a shallow, quiet pool over rubble and bedrock bottom except for a small area of mud bottom (backwater) above the point where a short riffle drains into this pool from Area 6 (Pl. 30, Fig. 1).

Area 6 has a length of 200 feet, an average width of 50 feet, and a maximum depth of one and one-half feet. This is a shallow, quiet pool over bedrock bottom, except for a small area of mud bottom at one side of the upper end of the pool. A short, steep, rubble-riffle is included in this area at the upstream end (Pl. 30, Fig. 2).

Areas 2, 4, and 7 resemble at least one of the areas described above but were sampled less intensively. Data from areas 2, 4, and 7 are included in discussion of the total fauna of the upper Neosho river but are excluded from the discussion of representative parts of that fauna.

Methods

Rotenone

Rotenone was applied to an intermittent pool in 1957. In 1958 and 1959 rotenone was applied to the upper end of a pool and mixed by agitating the water. The concentration in the pool was maintained by slowly introducing part of the rotenone into the riffle at the head of the pool. This was the most effective means of obtaining a large sample of fish from the deeper, slowly flowing water of the upper Neosho. Pools in which rotenone was used had areas of as much as one-half acre and depths in excess of six feet.

Shocker

In 1959 the shocker was used extensively in several areas of the upper Neosho. Because of the small size of the stream, "tennis-racket" electrodes were used effectively by two men—one carrying the electrodes and one picking up fish and placing them in a live-box. In fast water, many fish floated into a seine placed across the lower end of the area. A large segment of the population was collected in this manner. Areas in which fish were collected by means of the shocker included riffles, and pools having flowing water no more than three feet in maximum depth. The bottom-type was usually gravel, rubble or bedrock, but a small amount of mud bottom was present in many pools.

Because of the necessity of wading, we could not use the shocker effectively in water more than three feet deep. In addition, turbidity of the water prevented effective collection of stunned fish in the deeper pools. Therefore, rotenone was more effective in deep water than was the shocker. In shallow, swift riffles and pools, the shocker yielded more reliable samples than did rotenone, because of difficulty in maintaining adequate concentrations of rotenone where flow was swift.

The relative abundance of each species in the upper Neosho was calculated from cumulative results obtained by use of the shocker in seven areas in 1959. Population estimates were made by collecting fish with the shocker, marking them by clipping fins or staining them in Bismark Brown Y at a concentration of 1:20,000 (Deacon, 1961), returning them to the stream, and making a second collection three hours (Areas 1 and 3) or 24 hours (Area 6) later. The same area was shocked again within two to eight days. Collections throughout the one-half-mile section yielded information on movement.

Changes in the Fauna at the Upper Neosho Station, 1957 Through 1959.

The following discussion is based principally on collections made with rotenone in 1957, 1958 and 1959 (Table 12). Other supplementary data aid in understanding the changes that occurred after the resumption of normal flow at the upper Neosho station.

The population in 1957 was strongly dominated by black bullhead and young-of-the-year channel catfish. Other common species were long-eared sunfish, red shiner, yellow bullhead, orange-spotted sunfish and green sunfish. This fauna, with the exception of young-of-the-year individuals, was a fauna produced during the years of drought. Deacon and Metcalf (1961:318-321) found a similar fauna in streams of the Wakarusa River Basin that had been seriously affected by drought.

The black bullheads taken in 1957 were predominately yearlings. It is likely that by 1956 the total fish population in the upper Neosho had been decimated by drought. The ponded conditions prevalent in that year were conducive to production and survival of young black bullheads. Fig. 3 shows that this dominant 1956 year-class reached an average length of approximately 6.5 inches by August, 1959.

Reproduction by black bullheads was limited in 1957, 1958, and 1959, and slight reduction in relative abundance occurred from 1957 to 1958. The relative abundance in 1959 remained nearly stable. If stream-flow remains essentially continuous for the next few years, the number of black bullheads probably will decline as individuals of the 1956 year-class reach the end of their life-span.

Reference has been made to the large hatch of channel catfish in 1957, in a discussion of that species. Conditions for survival of young channel catfish at the upper Neosho station in 1957 were good because there was continuous flow over many gravel-rubble riffles, which were largely unoccupied by other fish, in the spring and summer of 1957.

TABLE 12. PERCENTAGE-COMPOSITION OF THE FISH-FAUNA AT THE UPPER NEOSHO STATION IN 1957, 1958 AND 1959, AS COMPUTED FROM COLLECTIONS OBTAINED BY USING ROTENONE.

SPECIES	1957	1958	1959
Big-mouthed Buffalo	...	T*	T
Small-mouthed Buffalo	...	...	T
River Carpsucker	T	0.8	1.8
Golden Redhorse	T	3.0	5.7
Creek Chub	...	T	0.8
Red-finned Shiner	1.3	3.0	0.8
Red Shiner	6.5	13.1	12.1
Ghost Shiner	T	T	...
Blunt-nosed Minnow	T	T	T
Fat-headed Minnow	T	T	1.4
Stoneroller	0.8	1.5	3.5
Black Bullhead	40.8	30.5	32.0
Yellow Bullhead	5.3	8.8	2.5
Channel Catfish	28.4	15.5	18.5
Flathead	T	T	T
Stonecat	T	T	1.4
Spotted Bass	T	T	0.8
Largemouth	T	T	T
Green Sunfish	3.1	6.8	6.4
Long-eared Sunfish	8.8	3.7	1.9
Orange-spotted Sunfish	3.1	8.9	2.5
Bluegill	T	T	T
White Crappie	T	...	T
Logperch	T	2.1	0.8
Slender-headed Darter	0.6	0.6	3.1
Orange-throated Darter	...	T	2.5
Total number of fish	786	965	513
Size of sample-area in acre-feet	.002	.33	.33

* T denotes less than one-half of one per cent of the population.

Channel catfish also showed a slight decline in relative abundance after 1957, resulting from mortality in the 1957 year-class. With continuous flow, channel catfish will probably remain abundant, although annual reproductive success probably will be less than in 1957.

The big-mouthed buffalo, small-mouthed buffalo, creek chub and orange-throated darter were not taken in 1957, but appeared in collections in 1958. The river carpsucker, golden redhorse, red shiner, fat-headed minnow, stoneroller, stonecat, and slender-headed darter also increased in abundance between 1957 and 1959. The increased abundance of all these species in 1958 and 1959 resulted in a more diversified fauna, with lesser predominance by any single species, than in 1957 (Table 12); this change is related to the increased, permanent flow in 1958 and 1959.

Local Variability of the Fauna in Different Areas at the Upper Neosho Station, 1959

The shallow areas in which the shocker was used in 1959 are the prevalent habitat in the upper Neosho River. The relative abundance of fishes found in these areas is presented in Table 13. The red shiner was most abundant and was followed (in decreasing order) by long-eared sunfish, minnows of the genus *Pimephales*, green sunfish, red-fined shiner, channel catfish, and stoneroller. Other species combined comprise less than ten per cent of the population.

Table 13 also shows the variability in relative abundance of different species among areas that have the same general kind of habitat. The species composition is similar in all areas. The sample obtained with rotenone in 1959 is included in Table 13 to show differences in the fauna of deep, slowly flowing areas and shallower areas with stronger current. The differences in relative abundance indicate the kind of habitat that each species is able to utilize most fully.

Golden redhorse and black bullhead were most abundant in large, deep, quiet pools (5.7 per cent and 32 per cent of the total population) and were more abundant in Area 5 (3.2 per cent and 7.3 per cent respectively) than in any of the other shallow areas. Area 5 has greater average depth, more mud bottom, and less riffle area than areas 1, 3 and 6.

The golden redhorse and black bullhead have specific habitat preferences that are not evident in the above discussion. My collections indicate that the golden redhorse prefers deep water having some current, whereas the black bullhead prefers little or no current.

Species that prevailed in or near riffles were: creek chub, sucker-mouthed minnow, stoneroller, channel catfish (young-of-the-year only), flathead (young-of-the-year only), stonecat, slender-headed darter, and orange-throated darter. Of these species, the sucker-mouthed minnow, slender-headed darter and orange-throated darter reached their greatest abundance at Area 3, where the riffle is shallow, slow, and has a bottom composed of flat limestone rubble.

The riffle at Area 1 is, for the most part, deeper and faster than at Area 3 and has a bottom composed of gravel and small rocks. The creek chub, stoneroller, channel catfish (young-of-the-year), flathead (young-of-the-year), and stonecat reached their greatest

TABLE 13. RELATIVE ABUNDANCE OF FISH (PER CENT OF TOTAL POPULATION MADE UP BY EACH SPECIES), IN THE FIRST COLLECTION MADE IN EACH OF FOUR DIFFERENT SHALLOW AREAS BY MEANS OF THE SHOCKER, IS SHOWN IN VERTICAL COLUMNS 1-4. RESULTS OF THE USE OF ROTENONE IN A FIFTH, DEEPER AREA ARE SHOWN IN COLUMN 5. COLUMN 6 COMBINES DATA FROM ALL COLLECTIONS MADE BY USING THE SHOCKER IN SEVEN SHALLOW AREAS (INCLUDING COLUMNS 1-4).

	Area 1	Area 3	Area 5	Area 6	Rotenone	All areas
Big-mouthed Buffalo	....	....	T*	....	T	T
Small-mouthed Buffalo	....	....	.6	....	T	T
River Carpsucker	....	T	10.6	T	1.8	.8
River Carpsucker (yy) **	....	.8	T	3.7	....	1.0
Short-headed Redhorse	....	....	.6	....	....	T
Golden Redhorse	.8	1.0	3.2	....	5.7	T
Carp	....	....	....	....	....	T
Golden Shiner	....	....	....	....	....	T
Creek Chub	1.6	T	T	T	.8	T
Sucker-mouthed Minnow	....	11.2	T	3.4	....	1.4
Red-finned Shiner	....	....	....	4.0	.8	8.1
Red Shiner	18.2	24.0	7.8	20.1	12.1	35.9
Sand Shiner	....	5.2	....	1.1	....	T
Pimephales (yy)	....	....	....	....	....	6.7
Mountain Minnow	....	....	....	T	....	T
Blunt-nosed Minnow	....	.8	4.1	11.7	T	3.4
Parrot Minnow	....	....	....	....	....	T
Fat-headed Minnow	T	T	3.4	12.1	1.4	2.6
Stoneroller	27.7	17.4	.6	5.8	3.5	5.1
Black Bullhead	2.1	T	7.3	T	32.0	.6
Yellow Bullhead	T	T	....	T	2.5	T
Channel Catfish (j)†	5.8	7.6	41.3	T	14.6	4.2
Channel Catfish (yy)	9.5	7.0	T	4.3	3.9	2.5
Flathead (j)	....	.8	2.1	T	T	T
Flathead (yy)	1.6	T	....	....	....	T
Stonecat	10.3	1.4	....	....	1.4	.7
Spotted Bass	....	T	.6	T	.8	T
Largemouth	....	....	T	....	T	T
Green Sunfish	11.2	3.5	5.9	12.2	6.4	10.1
Long-eared Sunfish	5.4	6.0	5.1	14.6	1.9	12.8
Orange-spotted Sunfish	T	T	1.4	1.8	2.5	.5
Bluegill	....	....	1.0	....	T	T
White Crappie	....	....	....	....	T	T
Logperch	T	T	T	T	.8	T
Slender-headed Darter	T	11.4	1.1	1.6	3.1	1.3
Orange-throated Darter	.8	1.8	T	.5	2.5	T
Freshwater Drum	....	....	T	....	....	T
Total number of fish	242	484	727	924	513	17,796
Area in square feet	840	6324	12500	10000	....	....
Volume	....	....	....	....	⅓ acre-foot	

* "T" designates species that comprised less than 0.5 per cent of the population.

** (yy) signifies young-of-the-year.

† (j) signifies yearlings or two-year-olds.

abundance in Area 1. All species that showed a preference for riffles were rare or absent in Area 5 where no riffle-habitat was sampled. The riffle-dwelling species that were present in collections made with rotenone in the deeper pools were taken from the riffle into which rotenone was introduced.

The river carpsucker, blunt-nosed minnow, fat-headed minnow, channel catfish (yearlings and two-year-olds), flathead (yearlings and two-year-olds), green sunfish and long-eared sunfish showed a preference for shallow, quiet water. All of these species were more common in collections from Areas 5 and 6 than in collections from other areas.

Temporal Variability of Fauna in the Same Areas

The variability of the population in successive collections from the same area is presented in Table 14. Supplementary data obtained in Areas 2, 4 and 7 support conclusions discussed below for Areas 1, 3 and 6. The abundance of some species maintained a constant level, whereas that of others varied.

TABLE 14. NUMBERS OF INDIVIDUALS COLLECTED BY MEANS OF THE SHOCKER AT VARYING INTERVALS IN SEPTEMBER, 1959. THE NUMBER AT THE TOP OF EACH COLUMN IS THE DATE WHEN THE COLLECTION WAS MADE.

SPECIES	Area 1			Area 3			Area 6		
	3	4	8	9	10	15	16	18	20
Golden Redhorse	2	2	.....	5	5	2	.....	.....	3
Creek Chub	4	3	7	1	.....	.....	1	2	.....
Sucker-mouthed Minnow	.....	.....	.....	54	42	25	31	7	6
Red-finned Shiner	.....	.....	1	.....	.....	4	31	13	4
Red Shiner	44	7	211	117	170	438	186	209	62
Blunt-nosed Minnow	.....	.....	.....	4	10	19	108	91	13
Fat-headed Minnow	1	.....	.....	1	2	3	112	156	48
Stoneroller	67	39	49	84	107	55	54	67	22
Black Bullhead	5	.....	1	2	1	.....	.....	3	7
Yellow Bullhead	1	1	.....	2	1	.....	1	.....	3
Channel Catfish	14	7	.....	36	16	.....	3	1	23
Channel Catfish (yy)*	23	16	17	34	34	22	40	23	28
Flathead	.....	.....	.....	4	8	1	2	.....	1
Flathead (yy)	4	1	1	2	1	1	.....	.....	.....
Stonecat	25	8	12	7	7	5	.....	.....	.....
Green Sunfish	27	17	12	13	16	17	62	62	74
Long-eared Sunfish	13	12	1	6	3	3	10	22	31
Logperch	1	.....	.....	2	.....	.....	.....	.....	.....
Slender-headed Darter	.. ..	1	2	55	45	23	15	1	1
Orange-throated Darter	2	1	2	9	11	8	5	.....	1
Total	233	115	316	438	480	626	661	657	347

* (yy) means young-of-the-year only.

Stoneroller, channel catfish (young-of-the-year), green sunfish, and long-eared sunfish formed the most stable element of the population, in that the numbers of these species varied less in successive collections than did numbers of other species.

The number of orange-throated darters remained constant at Areas 1 and 3, and the number of stonecats changed little in successive collections from Area 3. I suspect that an apparent decline in stonecats at Area 1 on September 4 was due to a slow rate of dispersal from the point of release (see pages 413, 414).

Some species (sucker-mouthed minnow, red-finned shiner, slender-headed darter, and fat-headed minnow) decreased significantly in successive samples from the same area because of mortality in handling or movement out of the area of initial capture.

The decrease in abundance of the sucker-mouthed minnow may have been due to some mobility of the species. Evidence for mortality caused by handling was obtained for the red-finned shiner and probably accounts for the reduction of this species in Area 6. The red-finned shiner is also probably a mobile species. The reduction in abundance of the slender-headed darter seems unexplainable because no evidence was obtained for either movement or mortality.

Fat-headed minnows also declined markedly in successive collections from Area 6, the only area in which the species was common. No marked fat-headed minnows were taken outside the area of release, indicating low mobility of the species. I cannot certainly account for their decline; possibly there was latent mortality due to shocking.

The numbers of red shiners, blunt-nosed minnows, and juvenile channel catfish varied erratically in successive collections, probably as a result of movement. This problem is discussed for all species in a later section.

Population-Estimation

The direct-proportion method was used to estimate fish populations in Areas 1, 3 and 6. Reliable results could not be obtained for all species because of scarcity, mortality in handling, mobility, or other factors.

A high rate of mortality due to handling was observed in Area 1 for the red shiner and in Area 6 for river carpsucker (young-of-the-year), sucker-mouthed minnows, red-finned shiner, red shiner, blunt-nosed minnow, and stoneroller. In Area 3, in contrast, there was little mortality in the same species during the twelve-hour interval that fish were held in traps prior to release as marked individuals.

The following species were common in at least one area, but probably are sufficiently mobile (see page 416) to invalidate estimates of static populations in small areas: red shiner, red-finned shiner, and channel catfish (yearlings and older). Other species were rare and are indicated as "T" in Table 13.

Those species for which population-estimates seem warranted include: golden redhorse, sucker-mouthed minnow, red shiner, sand shiner, fat-headed minnow, stoneroller, stonecat, channel catfish (young-of-the-year), green sunfish, long-eared sunfish, slender-headed darter, and orange-throated darter. I consider the estimate valid if a high percentage of the marked fish is recaptured. Results are presented in Table 15, and ordinarily will not be referred to in the following discussion of the population in each of the three areas.

Area 1

The order of abundance at Area 1, in terms of the estimated population per 500 square feet, was as follows: stoneroller (47.6), stonecat (29.4), channel catfish (young-of-the-year) (20.6), green sunfish (19.4), red shiner (18.2), long-eared sunfish (9.4), channel catfish (yearlings and older) (6.5), golden redhorse (1.2). Insufficient data make inclusion of other species unreliable.

A comparison of the order of abundance between the estimated total population and the percentage composition in the first collection from each area shows significant correlations. The percentage-composition of the fish fauna at Area 1 was calculated as follows: stoneroller (27.7%), red shiner (18.2%), green sunfish (11.2%), stonecat (10.3%), channel catfish (young-of-the-year) (9.5%), channel catfish (yearlings and older) (5.8%), long-eared sunfish (5.4%), golden redhorse (0.8%). It can be seen that the stoneroller, green sunfish, long-eared sunfish and golden redhorse follow each other in the same order in both calculations. The stonecat is shown to be more common than channel catfish (young-of-the-year) in both calculations, but both species appear to be more abundant than green sunfish and red shiner in calculations of the total population and less abundant in the percentage-composition in the first collection. I think that the order of abundance as shown by percentage-composition is the more accurate figure for Area 1. The abundance of the red shiner is known to have been affected by mortality in collecting. Furthermore, as will be shown later, the species is so mobile that its abundance often changes markedly in a short time. Therefore, it is not surprising to find the red shiner in widely varying positions of relative and absolute abundance. However, the green sunfish maintains stable populations and should remain in about the same position of abundance in relation to other species (such as the stonecat and channel catfish young-of-the-year) that also maintain stable populations. The differences in order of abundance obtained by the two methods for green sunfish and channel catfish young-of-the-year are not great. However, in the estimation of total population the abundance of the stonecat seems significantly greater, in relation to other species, than in the calculation of percentage-composition. I believe that this difference can be attributed to the relatively

TABLE 15. DATA USED IN ESTIMATING TOTAL POPULATIONS, BY DIRECT

SPECIES	Number captured first collection			Number marked and released			Number captured second collection		
	1	3	6	1	3	6	1	3	6
Golden Redhorse	2	5	0	2	5	0	2	5	0
Sucker-mouthed Minnow	0	54	31	0	51	15	0	42	12
Red Shiner	44	116	186	22	106	86	7	165	202
Sand Shiner	0	25	10	0	25	7	0	35	10
Blunt-nosed Minnow	0	4	108	0	3	28	0	10	91
Fat-headed Minnow	1	1	112	1	1	101	0	2	156
Stoneroller	67	84	54	58	79	33	39	107	67
Channel Catfish (j)†	14	37	3	9	32	3	7	16	1
Channel Catfish (yy)*	3	34	40	22	33	39	16	34	23
Stonecat	25	7	0	25	7	0	8	7	0
Green Sunfish	27	‡—	62	27	—	62	17	—	62
Long-eared Sunfish	13	6	10	13	6	10	12	3	22

† (j) Denotes juveniles only.
* (yy) Denotes young-of-year only.
‡ A dash denotes incomplete or insufficient data.

low number of marked fish recaptured, which is probably due to a slow rate of dispersal from the point of release. Stonecats were released in relatively quiet water, and if they remained there they might be missed in subsequent collections, because they lack air-bladders and tend to remain on the bottom when shocked. Therefore, the calculated total population of the stonecat in Area 1 may be too high.

Area 3

The order of abundance of the species at Area 3, in terms of the estimated population per 500 square feet, was as follows: red shiner (77.1), stoneroller (19.2), sucker-mouthed minnow (10.0), channel catfish (young-of-the-year) (8.1), sand shiner (5.8), channel catfish (yearlings and older) (3.1), long-eared sunfish (0.5), golden redhorse (0.4). Insufficient data make inclusion of other species unreliable.

For comparison with the estimates of total population, the percentage-composition in the first collection gives the following results: red shiner (24.0%), stoneroller (17.4%), sucker-mouthed minnow (11.2%), channel catfish (yearlings and older) (7.6%), channel catfish (young-of-the-year) (7.0%),

PROPORTIONS, IN AREAS 1, 3, AND 6 AT THE UPPER NEOSHO STATIONS.

Number of marked fish recaptured			Estimated total population			Percent of marked fish recovered			Number per 500 square feet		
1	3	6	1	3	6	1	3	6	1	3	6
2	5	0	2	5	0	100	100	—	1.2	.4	0
0	17	0	0	126	—	—	33	0	0	10.0	—
5	18	14	31	972	1284	23	17	11	18.2	77.1	64
—	12	1	0	73	—	—	48	—	0	5.8	—
0	1	8	0	—	319	—	33	28	0	—	16
0	0	19	—	—	830	0	0	19	—	—	41.5
28	35	8	81	242	276	48	44	24	47.6	19.2	13.8
6	13	0	11	39	—	67	41	0	6.5	3.1	—
10	11	1	35	102	—	45	33	3	20.6	8.1	—
4	1	—	50	—	0	16	14	—	29.4	—	0
14	—	22	33	—	175	52	—	35	19.4	—	8.8
10	3	6	16	6	37	76	50	60	9.4	.5	1.9

long-eared sunfish (6.0%), sand shiner (5.2%), and golden redhorse (1.0%).

For the most part, the species have the same order of abundance in both methods of analysis. Those that are apparently out of order are channel catfish (yearlings and older) and long-eared sunfish. The first species is mobile (excepting young-of-the-year) and commonly fluctuates widely in numbers in the same area; the second species was treated differently in that only adults were considered in the population-estimation whereas both young and adults were considered in calculating percentage-composition. (I found that I could not confidently distinguish between young-of-the-year of green sunfish, long-eared sunfish and orange-spotted sunfish after staining.)

Area 6

The order of abundance of the species at Area 6, in terms of the estimated population per 500 square feet, was as follows: red shiner (64.0), fat-headed minnow (41.5), blunt-nosed minnow (16.0), stoneroller (13.8), green sunfish (8.8), long-eared sunfish (1.9). Insufficient data make inclusion of other species unreliable.

Calculations of percentage-composition give the following results: red shiner (20.1%), long-eared sunfish (14.6%), green sunfish (12.2%), fat-headed minnow (12.1%), blunt-nosed minnow (11.7%), stoneroller (5.8%). The two species of sunfish form a more significant part of the population in the latter analysis because young are included. Only adults were considered in the estimation of total population.

The fact that estimates of the total population and the percentage-composition agree in most respects lends support to the validity of both methods of analysis. It should be re-emphasized that differences in the order of abundance in the various areas reflect the ability of each species to utilize each particular kind of habitat.

Movement of Marked Fish

Some measure was gained of the amount of movement exhibited by several species of fish. Results are biased in favor of a conclusion that a species is sedentary because a large percentage of the recaptures were made in collections taken in the same immediate area three hours after release of marked fish, the total area checked was not large (one mile), and collecting was limited to an eleven-day period. Nevertheless, some species were shown to be definitely mobile and others exhibited pronounced sedentary tendencies. The results of experiments on movement are presented in Table 16. Marked fish (dyed and fin-clipped) were taken as long as seven days after being marked. Only those species in which more than ten individuals were marked are included.

TABLE 16. DATA ON MOVEMENT OF MARKED FISH AT THE UPPER NEOSHO STATION, SEPTEMBER, 1959.

SPECIES	Number marked	Number re-captured	Number moved upstream	Number moved down-stream
Golden Redhorse	24	16	0	2
Sucker-mouthed Minnow	68	27	7	0
Red-finned Shiner	74	0	0	0
Red Shiner	1326	152	48	25
Blunt-nosed Minnow	136	32	1	10
Fat-headed Minnow	151	40	0	0
Stoneroller	177	90	1	0
Black Bullhead	25	6	2	0
Channel Catfish (j)†	294	36	4	7
Channel Catfish (yy)*	145	34	2	0
Stonecat	33	6	0	0
Green Sunfish	124	68	1	0
Long-eared Sunfish	33	21	0	0
Slender-headed Darter	70	1	0	0
Orange-throated Darter	13	0	0	0

† (j) denotes juveniles only.
* (yy) denotes young-of-year only.

Blunt-nosed minnow, red shiner, and channel catfish (yearlings and older) are more mobile than other species.

The mobility of channel catfish has been discussed by Muncy (1958) and Funk (1957). My records show that of 36 marked channel catfish that were recaptured, 11 were taken in areas other than the one into which they had been returned. A pronounced mobile tendency on the part of the red shiner and blunt-nosed minnow is shown by the fact that of 152 marked red shiners recaptured, 73 had moved from the area of release; and of 32 marked blunt-nosed minnows recaptured, 11 had moved from the area of release. The fact that the habitat occupied by these species is not precise (ranging from swift riffles to quiet pools) supports a conclusion that the species are mobile.

The fat-headed minnow, stoneroller, channel catfish (young-of-the-year), green sunfish and long-eared sunfish form a sedentary element of the population. With the exception of the fat-headed minnow, the sedentary group also maintained relatively stable numbers in Areas 1, 3 and 6 throughout the study (Table 14). It is interesting to note that, in contrast to the mobile group, the species forming the sedentary group have rather well-defined habitat preferences.

A third group of species, represented by the red-finned shiner, stonecat, slender-headed darter and orange-throated darter, was characterized by having a low rate of recapture. I suspect that mortality is a factor contributing to the failure to recapture red-finned shiners, because in one collection only four of 31 red-finned shiners captured were successfully marked and released, in another case 70 of 818. The red-finned shiner occurs most often in pools but is also taken in other areas, is pelagic, and probably is a mobile species.

The stonecat, slender-headed darter and orange-throated darter are generally restricted to riffle-habitats, and are probably sedentary. The low number of recaptures for these three species probably is due either to a slow rate of dispersal from the point of release or to latent mortality resulting from shock. Table 14 shows that these three species maintain comparatively stable populations, but there seems to be a tendency for a reduction in numbers with continued collecting, even though all fish captured were returned to the stream.

Golden redhorse showed a high rate of recapture. All individuals marked were recaptured three hours after release in Areas 1 (two fish) and 3 (five fish). Nine individuals were taken from Area 4 on 11 September; seven of these were marked and released in the next pool downstream (Area 3). On 15 September, two fish were retaken in Area 3 and two were retaken in Area 2, the next pool downstream. The species was common in Area 5 also where five of eight marked individuals were recaptured two days after release. It seems that the golden redhorse is somewhat restricted in movement, at least for short periods.

The sucker-mouthed minnow and black bullhead showed some movement—less than such mobile species as red shiners and channel catfish, but more than the sedentary group. Seven of 27 marked sucker-mouthed minnows were taken in areas adjacent to the one to which they had been returned. Two of six black bullheads that were recaptured had moved. The black bullhead moved the greater distance. The extent of short-term movement by several of the species in the Upper Neosho correlates well with redistribution subsequent to drought in the Wakarusa River, discussed by Deacon and Metcalf (1961).

Similarity of the Fauna at the Upper Neosho Station to the Faunas of Nearby Streams

The fauna that I found to be characteristic at the upper Neosho station has affinity with the upland tributary-fauna described by Metcalf (1959) for Chautauqua, Cowley and Elk Counties, Kansas. The primary difference is a nearly complete absence at my station of the Ozarkian element of the population. Some species (red-finned shiner, long-eared sunfish, and spotted bass) listed by Metcalf as characteristic of the mainstream of smaller rivers occur at the upper Neosho station in greater abundance then elsewhere in the Neosho. This difference is probably due to the fact that the upper Neosho station is somewhat larger and slightly more turbid than Metcalf's "upland tributaries."

Hall (1952) reported on the distribution of fishes in the vicinity of Fort Gibson Reservoir, an impoundment on the Grand (Neosho) River in Oklahoma. He separated the fishes into three groups according to habitat-preference: species restricted to upland tributaries on the east side of Grand (Neosho) River, species restricted to lowland tributaries on the west side of Grand (Neosho) River, and species occurring in the Grand River proper and/or tributaries on one or both sides.

Several species found in the upper Neosho River also occur in the area studied by Hall. Of these, only the creek chub was restricted to upland tributaries on the east side of Grand (Neosho) River. The sucker-mouthed minnow and red-finned shiner were restricted to the lowland tributaries on the west side of Grand (Neosho) River in the Fort Gibson Reservoir Area. Golden redhorse, stoneroller, yellow bullhead, spotted bass, green sunfish, long-eared sunfish, and orange-throated darter were present in collections from the Grand River proper and/or tributaries on both sides of the river, most commonly in tributaries.

Hall's data show that black bullhead, large-mouthed bass, white crappie, and logperch occurred most frequently in or near the quiet water of the reservoir. In my study these fish were most common in the larger, quiet pools at the upper Neosho station.

COMPARISON OF THE FISH FAUNAS OF THE NEOSHO AND MARAIS DES CYGNES RIVERS

The Marais des Cygnes River has less gradient (especially in the upstream portions), fewer and shorter riffles, and more mud bottom than does the Neosho River. Stream-flow during drought was reduced to a proportionately greater degree in the Neosho River than it was in the Marais des Cygnes River. Average flow of the Neosho River near Parsons (drainage area: 4905 square miles), Kansas, was less than average flow of the Marias des Cygnes River at Trading Post (drainage area: 2880 square miles), Kansas, in 1953, 1955 and 1956. In normal times the Neosho River carries a larger volume of water than the Marais des Cygnes. The Neosho River has a greater variety of habitat-conditions and a more diversified fish-fauna than the Marais des Cygnes.

The following species were taken in the Neosho River but not in the Marais des Cygnes River: blue sucker, high-finned carpsucker, golden redhorse, gravel chub, mimic shiner, mountain minnow, parrot minnow, Neosho madtom (the only endemic in either river), mosquitofish, spotted bass, smallmouth, black crappie, logperch and fan-tailed darter. Most of the above species are usually found in association with gravel-bottom, which is prevalent in Neosho River. The blue sucker, high-finned carpsucker, gravel chub, mountain minnow, and parrot minnow normally occur in the larger streams in Kansas. The last three species became more abundant in the Neosho River following resumption of flow. The golden redhorse also increased in abundance from 1957 to 1959, but was most numerous at the upper Neosho station, whereas the other species occurred mainly at the lower stations.

The mimic shiner, spotted bass, smallmouth, and fan-tailed darter are characteristic of upstream habitats with clear water (tributaries, rather than the mainstream), and were taken in the Neosho River only in 1957 *or* became less abundant from 1957 to 1959.

The silver chub, slender madtom and tadpole madtom were taken in the Marais des Cygnes River only in 1957 and were not taken in the Neosho River.

The following species, common to both rivers, were more abundant in the Neosho: long-nosed gar, short-nosed gar, river carpsucker, creek chub, sucker-mouthed minnow, red-finned shiner, red shiner, ghost shiner, blunt-nosed minnow, fat-headed minnow, stoneroller, yellow bullhead, channel catfish, flathead, stonecat, largemouth, long-eared sunfish, slender-headed darter, and fresh-water drum. These species, collectively, reflect the more diversified habitats (more gravel-bottom, more riffle-areas, more gradient, greater range of stream-size sampled) in the Neosho River.

The following species, common to both rivers, were more abundant in the Marais des Cygnes: gizzard shad, carp, sand shiner, black bullhead and white crappie. These species (with the exception of sand shiner) emphasize the fact that the Marais des Cygnes is a sluggish stream with large areas of mud bottom. Differences in the abundance of the sand shiner in the two rivers are part of taxonomic and distributional studies being conducted by Mr. Bernard C. Nelson.

The following species were not consistently more abundant in one river than the other: big-mouthed buffalo, black buffalo, small-mouthed buffalo, short-headed redhorse, green sunfish, orange-spotted sunfish and orange-throated darter. These species, excepting the orange-throated darter and short-headed redhorse, occurred in a wide variety of habitats.

FAUNAL CHANGES, 1957 THROUGH 1959

The following species increased in abundance from 1957 to 1959 (Tables 10 and 11): long-nosed gar, short-nosed gar, river carpsucker, creek chub, gravel chub, sucker-mouthed minnow, mountain minnow, blunt-nosed minnow, parrot minnow, stoneroller, stonecat, Neosho madtom, green sunfish, slender-headed darter, and orange-throated darter.

These species can be separated into three groups, characteristic of different habitats but having in common a preference for permanent flow. One group, composed of long-nosed gar, short-nosed gar, river carpsucker, gravel chub, mountain minnow, parrot minnow, and Neosho madtom, prefers streams of moderate to large size.

A second group composed of creek chub, sucker-mouthed minnow, stoneroller, and orange-throated darter occurs most abundantly in small, permanent streams. The green sunfish may be included here on the basis of its abundance at the upper Neosho station; however, this is a pioneer species and does not require permanent flow.

The third group is characteristic of continuously flowing water, but in both upstream and downstream situations. The species in this group (blunt-nosed minnow, stonecat, and slender-headed darter), increased in response to a resumption of permanent flow, but did not respond as quickly as did channel catfish, flatheads and freshwater drum, which are discussed subsequently.

The fact that riffle-insects were abundant throughout my study convinces me that food was not a limiting factor in the re-establishment of the fish-fauna on riffles of the Neosho River.

The following species decreased in abundance during my study (Tables 10 and 11): gizzard shad, carp, rosy-faced shiner, blunt-faced shiner, red shiner, mimic shiner, black bullhead, yellow bullhead, channel catfish, flathead, slender madtom, tadpole madtom, freckled madtom, spotted bass, largemouth, black crappie, fan-tailed darter, and freshwater drum.

Among the species that decreased, three groups, characteristic of different habitats, can be distinguished. The first group occurs most commonly in ponded conditions or in slowly flowing streams. Species in this group are: shad, carp, black bullhead, tadpole madtom, largemouth, black crappie, and white crappie. Bullhead, bass and crappie commonly occur in farm ponds and lakes in Kansas and seem less well adapted to streams. It is therefore not surprising to find that these species decreased in abundance when flow was resumed.

A second group, composed of rosy-faced shiner, blunt-faced shiner, mimic shiner, slender madtom, freckled madtom, spotted bass, and fan-tailed darter, normally is characteristic of clear tributaries rather than the mainstream of rivers. These species probably used the mainstream as a refugium during drought; with the resumption of flow, conditions became unsuitable for these populations in the mainstream. At the same time, conditions probably became favorable to the re-establishment of these species in tributaries. Metcalf (1959:396) listed the rosy-faced shiner, blunt-faced shiner and mimic shiner as species that were characteristic of upland tributaries in the Flint Hills and Chautauqua Hills of Chautauqua, Cowley and Elk counties in Kansas. The slender madtom and fan-tailed darter are more common in clear streams of southeast Kansas than in other areas of the state (Cross, personal communication and data of the State Biological Survey of Kansas). Both species are recorded by Hall (1952:57-58) only in upland tributaries on the east side of Grand (Neosho) River in the Fort Gibson Reservoir area of Oklahoma. Neither species was taken in faunal studies of the Verdigris River in Oklahoma (Wallen, 1958), in the Verdigris and Fall rivers in Kansas (Schelske, 1957), or by Metcalf (1959).

The spotted bass is not so restricted in its distribution and its habitat-requirements as are other species in this group; but, in Kansas, spotted bass are most abundant in clear creeks in the southeast part of the state.

The freckled madtom was taken in most of the studies cited above and is most common in the smaller streams of the southeast one-fourth of Kansas and the northeast one-fourth of Oklahoma. Schelske (1957:47) reports that the freckled madtom was taken only in March, April, October and November in the Verdigris River, Kansas. My only record of this species was obtained in the Neosho River in April, 1958.

The third group is composed of channel catfish, flathead, and freshwater drum. This group represents that element of the population that responded most quickly to the resumption of continuous flow. The fact that adult channel catfish and flatheads live in pools and do not require flowing water to spawn gives these species a survival advantage as well as a reproductive advantage over obligatory riffle fishes (such as most darters) in the highly variable conditions found in Kansas streams. These factors resulted in unusually high reproductive success in 1957. Subsequent survival of fry was excellent; however, some mortality in the highly-dominant 1957 year-class became apparent in the 1958 and 1959 collections, accounting for a numerical decline in these species. The ability to respond immediately to increased flow is an adaptive feature that allows these species to maintain high levels of abundance in the highly fluctuating streams of Kansas.

The continuous flow that occurred in 1957 in the Neosho and Marais des Cygnes rivers, for the first time in four years, provided the necessary habitat for survival of young catfish hatched in that

Fig. 1. Neosho River, Middle Station, Sec. 3 and 4, T. 24 S., R. 17 E., looking upstream, July, 1958.

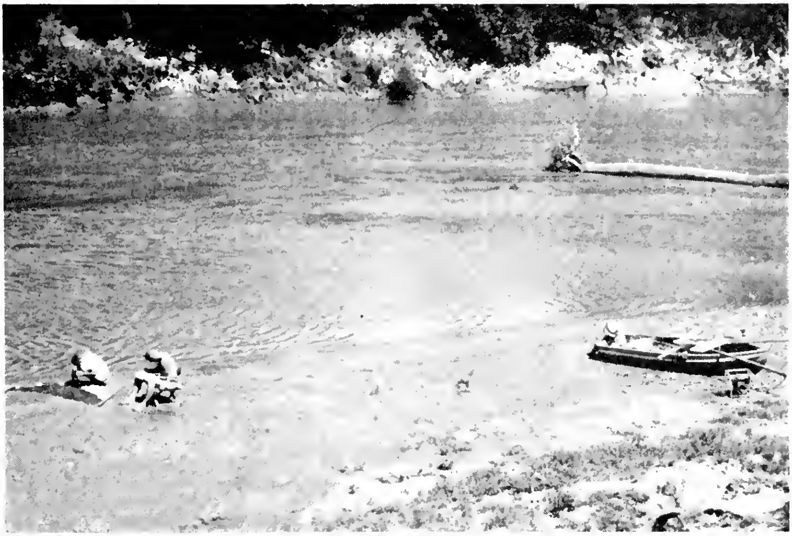

Fig. 2. Neosho River, Lower Station, Sec. 16, T. 29 S., R. 20 E., along gravel bar, July, 1959.

Fig. 1. Marais des Cygnes River, Upper Station, Sec. 12, T. 17 S., R. 17 E., looking downstream, June, 1960.

Fig. 2. Marais des Cygnes River, Middle Station, Sec. 6, T. 17 S., R. 20 E., looking downstream, June, 1960.

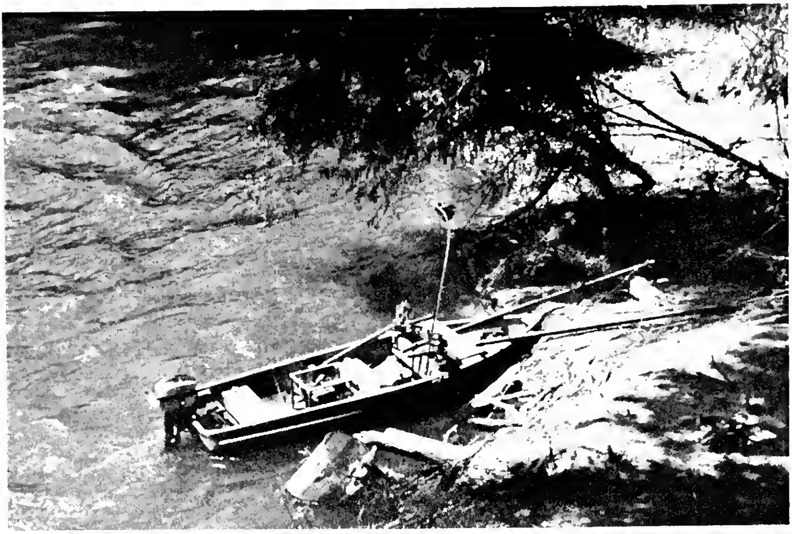

FIG. 1. Electrical fishing gear used at night.

FIG. 2. Pool at the upper Neosho station in which rotenone was used, Sec. 33, T. 15 S., R. 8 E., looking downstream, June, 1960.

FIG. 1. Area 1, upper Neosho station, Sec. 33, T. 15 S., R. 8 E., looking upstream, June, 1960.

FIG. 2. Area 3, upper Neosho station, Sec. 10, T. 16 S., R. 8 E., looking downstream, June, 1960.

year. The nearly complete absence of other species on the riffles, and the abundant populations of riffle-insects that I observed in the summer of 1957, were undoubtedly factors contributing to the survival of young.

The decrease in abundance of the red shiner may be partially due to an increase in the numbers of other species that are well adapted to conditions of permanent flow. At the completion of my study, the red shiner was still the most abundant minnow in both rivers. In 1957 this species was common in many habitats, including swift riffles, that were later occupied by madtoms, darters, the gravel chub, mountain minnow and sucker-mouthed minnow.

The basic pattern of change was clearly an increase in the species that are characteristic of permanently flowing waters, and a decrease in the species that are characteristic of ponds or small, clear streams.

CONCLUSIONS

The fauna of the Neosho and Marais des Cygnes rivers is capable of a wide range of adjustment in response to marked environmental changes. As these rivers become low and clear they take on many of the faunal characteristics of smaller tributaries and ponds. Species such as black bullhead, spotted bass, largemouth, white crappie, red shiner, rosy-faced shiner, blunt-faced minnow, mimic shiner, and slender madtom assume a more prominent position in the total population. Other species such as channel catfish, flathead, freshwater drum, blue sucker, and such riffle-dwelling species as the gravel chub, Neosho madtom, and slender-headed darter hold a less prominent position in the total population.

When permanent flow is re-established the more mobile and the more generalized species (with respect to habitat) are able to utilize the available space immediately. As a result, these species increase rapidly in numbers. This increase occurs both by movement from more permanent waters and by reproduction. Channel catfish, flathead, freshwater drum, and river carpsucker are mobile species (Funk, 1957; Trautman, 1957) and long-nosed gar probably are mobile. Individuals that move supplement those that survive in residual pools, and provide brood stock adequate to produce a large year-class in the first year of permanent flow.

The five species last mentioned are found in diverse kinds of streams, indicating that they are adaptable to varying habitats. A sixth species, the red shiner, although probably less mobile, is able to utilize opportunistically nearly any kind of habitat in

Plains streams. Although this species seldom is abundant in riffles, it was, in 1957, abundant in both pool and riffle situations at all my stations. These riffles were almost unoccupied by other species in 1957 until mid-summer, when hatches of channel catfish and flatheads occurred. Although adult channel catfish and flatheads live well in pools, the young occupy mainly riffles. This age- and size-segregation, in different habitats, was an advantage to the rapid re-establishment of these species in the Neosho and Marias des Cygnes rivers in 1957.

Species that occupy restricted habitats, especially riffle-dwellers such as the Neosho madtom, gravel chub, and slender-headed darter, were slowest to increase following drought. These species seem less capable of adapting to the variable conditions prevalent in the Neosho and Marais des Cygnes rivers than species that have more generalized habitat-requirements.

In the Neosho and Marais des Cygnes rivers nearly all species that were found in years just prior to the drought of 1952-1956 were again found in the last year of my survey; however, some species that live in a restricted habitat may eventually be extirpated in these two rivers. The high-finned carpsucker *Carpiodes velifer,* common shiner *Notropis cornutus*, horny-headed chub *Hybopsis biguttata*, and johnny darter *Etheostoma nigrum* all have specific habitat requirements and have disappeared or become restricted to one tributary in the Wakarusa River System (Deacon and Metcalf, 1961). The disappearance or reduction of these species implies long-term changes in the environment.

Suckers, minnows and catfishes constitute the main fauna of the Neosho and Marais des Cygnes rivers, because these families contain many species that have generalized habitat-requirements. Many of these fish are able to live successfully in either ponds or flowing waters and others are capable of long migrations. Because these fish predominate in the streams of Kansas, attempts should be made to utilize them more effectively.

In years such as 1957, large numbers of young channel catfish could be collected and used to stock new ponds and lakes. So doing would not affect the numbers of *adults* produced in the stream, and, if enough young could be removed, those remaining in the streams might grow faster.

Suckers and carp are abundant in the two rivers and mostly are unused at present, because current regulations preclude the use of methods effective for the capture of these species.

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FIG. 1. Area 5, upper Neosho station, Sec. 3, T. 16 S., R. 8 E., looking upstream, June, 1960.

FIG. 2. Area 6, upper Neosho station, Sec. 3, T. 16 S., R. 8 E., looking upstream, June, 1960.

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28-7576

(Continued from inside of front cover)

Vol. 8. Nos. 1-10 and index. Pp. 1-675, 1954-1956.

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1. Speciation of the wandering shrew. By James S. Findley. Pp. 1-68, 18 figures in text. December 10, 1955.
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10. A new bat (Genus Leptonycteris) from Coahuila. By Howard J. Stains. Pp. 353-356. January 21, 1957.
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18. Conspecificity of two pocket mice, Perognathus goldmani and P. artus. By E. Raymond Hall and Marilyn Bailey Ogilvie. Pp. 513-518, 1 map. January 14, 1960.
19. Records of harvest mice, Reithrodontomys, from Central America, with description of a new subspecies from Nicaragua. By Sydney Anderson and J. Knox Jones, Jr. Pp. 519-529. January 14, 1960.
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23. Speciation and evolution of the pygmy mice, genus Baiomys. By Robert L. Packard. Pp. 579-670, 4 plates, 12 figures in text. June 16, 1960.

Index. Pp. 671-690.

Vol. 10.
1. Studies of birds killed in nocturnal migration. By Harrison B. Tordoff and Robert M. Mengel. Pp. 1-44, 6 figures in text, 2 tables. September 12, 1956.
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(Continued on outside of back cover)

(Continued from inside of back cover)

8. Natural history of the salamander, Aneides hardyi. By Richard F. Johnston and Gerhard A. Schad. Pp. 573-585. October 8, 1959.
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Index. Pp. 611-626.

Vol. 11. 1. The systematic status of the colubrid snake, Leptodeira discolor Günther. By William E. Duellman. Pp. 1-9, 4 figures. July 14, 1958.
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Index Pp. 671-703.

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BY

ROBERT G. WEBB

UNIVERSITY OF KANSAS
LAWRENCE
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Vol. 7.
- *1. Mammals of Kansas. By E. Lendell Cockrum. Pp. 1-303, 73 figures in text, 37 tables. August 25, 1952.
- 2. Ecology of the opossum on a natural area in northeastern Kansas. By Henry S. Fitch and Lewis L. Sandidge. Pp. 305-338, 5 figures in text. August 24, 1953.
- 3. The silky pocket mice (Perognathus flavus) of Mexico. By Rollin H. Baker. Pp. 339-347, 1 figure in text. February 15, 1954.
- 4. North American jumping mice (Genus Zapus). By Phillip H. Krutzsch. Pp. 349-472, 47 figures in text, 4 tables. April 21, 1954.
- 5. Mammals from Southeastern Alaska. By Rollin H. Baker and James S. Findley. Pp. 473-477. April 21, 1954.
- 6. Distribution of Some Nebraskan Mammals. By J. Knox Jones, Jr. Pp. 479-487. April 21, 1954.
- 7. Subspeciation in the montane meadow mouse, Microtus montanus, in Wyoming and Colorado. By Sydney Anderson. Pp. 489-506, 2 figures in text July 23, 1954.
- 8. A new subspecies of bat (Myotis velifer) from southeastern California and Arizona. By Terry A. Vaughan. Pp. 507-512. July 23, 1954.
- 9. Mammals of the San Gabriel mountains of California. By Terry A. Vaughan. Pp. 513-582, 1 figure in text, 12 tables. November 15, 1954.
- 10. A new bat (Genus Pipistrellus) from northeastern Mexico. By Rollin H. Baker. Pp. 583-586. November 15, 1954.
- 11. A new subspecies of pocket mouse from Kansas. By E. Raymond Hall. Pp. 587-590. November 15, 1954.
- 12. Geographic variation in the pocket gopher, Cratogeomys castanops, in Coahuila, Mexico. By Robert J. Russell and Rollin H. Baker. Pp. 591-608. March 15, 1955.
- 13. A new cottontail (Sylvilagus floridanus) from northeastern Mexico. By Rollin H. Baker. Pp. 609-612. April 8, 1955.
- 14. Taxonomy and distribution of some American shrews. By James S. Findley. Pp. 613-618. June 10, 1955.
- 15. The pigmy woodrat, Neotoma goldmani, its distribution and systematic position. By Dennis G. Rainey and Rollin H. Baker. Pp. 619-624, 2 figures in text. June 10, 1955.

Index. Pp. 625-651.

Vol. 8. Nos. 1-10 and index. Pp. 1-675, 1954-1956.

(Continued on inside of back cover)

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North American Recent Soft-shelled Turtles (Family Trionychidae)

BY

ROBERT G. WEBB

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CONTENTS

INTRODUCTION

Is it true that the greater the degree of resemblance between two populations the shorter the time the two have been spatially isolated? Are aquatic environments more stable than terrestrial environments? These questions occurred to me while I was collecting turtles from river systems of the Gulf Coast. As a general rule, each kind of turtle seemed to occur throughout one continuous river system or large tributary, and with no barriers to dispersal therein and with the lapse of enough time for a population to reach its limits of dispersal, the question arose, "Where do subspecies and zones of intergradation occur"? It seemed logical to think that each isolated and continuous aquatic environment would not contain more than one subspecies of the same species. In terrestrial environments subspecies and transitions between them were recognizable. Terrestrial habitats were continuous for longer distances than the isolated, aquatic habitats. But, different species of turtles prefer different kinds of aquatic habitats. Also, barriers occur in large drainage systems, such as the Mississippi, where, in general, the western tributaries are sluggish, turbid and shallow, and the eastern tributaries are fast-flowing, clear and deep. But in young, relatively small, river systems that do not traverse radically different physiographic regions, and that show no gross ecological differences, habitats or microhabitats that do exist probably are only partial barriers and seem not to prevent the dispersal of most kinds of aquatic turtles. Consequently, it seemed that study of the degree of difference between closely related populations of turtles that occurred in one drainage system, or in adjacent drainage systems would indicate the length of time, respectively, that the drainage system had been continuous or the length of time that two or more systems had been isolated from one another.

Rivers or series of river systems having endemic kinds of turtles or having the most kinds of turtles that are different from those in adjacent rivers may be the oldest geologically, or may have been isolated the longest. Knowledge of the kinds of turtles and their relationships and distribution could indicate chronological changes in aquatic habitats. Of course, modifying factors such as differences between populations of turtles in rates of evolutionary change, degrees of vagility, rates of dispersal, and overland migrations need to be taken into account.

My accumulation of data on soft-shelled turtles was begun in the early nineteen-fifties. Although American softshells have been discussed in a revisionary manner by Agassiz (1857), Siebenrock (1924), Stejneger (1944) and Neill (1951), the relationships of all the component populations have not hitherto been appreciated. The present account attempts to combine in one publication what is known concerning the taxonomy, geographic distribution, life history, and relationships of the Recent American species and subspecies of the genus *Trionyx.*

Collecting Methods

Nocturnal collecting, by hand, from a boat that was nosed among brush piles along the shore line of rivers (Chaney and Smith, 1950: 323) in the early 1950's on rivers of the Gulf Coast drainage east of Texas yielded many turtles of the genus *Graptemys* but few softshells. Chaney and Smith (*loc. cit.*) reported only one softshell among 336 turtles taken in 21 collecting hours on July 5, 6 and 7 on the Sabine River; Cagle and Chaney (1950:385), however, recorded 11.6 per cent softshells of 208 turtles (collecting time not stated) taken on the Caddo Lake Spillway in Louisiana. Using hoop-nets is probably the most efficient method for collecting softshells considering the time and effort involved, and is the chief method I have used. Lagler (1943a:24) mentioned the use of watermelon rind as an effective bait. Kenneth Shain (field notes) trapped *T. spinifer emoryi* in hoop-nets baited with bread. I have used chopped fresh fish with most success; canned sardines have also been satisfactory. These baits seem to be more successful for trapping *spinifer* than they are for *muticus.* Hoop-nets were used to trap turtles in Lake Texoma, Oklahoma, from June 14 to July 2, 1954. The number of traps (usually four, rarely five) and trapping success varied with location. Of 156 turtles, 19 (12%) were *T. spinifer* and one was *T. muticus.*

Trotlines and set lines frequently catch softshells; sport fishermen often complain of catching these turtles on hook and line. Live worms, soft-bodied insects, small crawfish, minnows, small pieces of fish and other kinds of meat are adequate bait. Capture depends on the skill of attachment of the bait and the size of hook used. In my experience, softshells (mostly *spinifer*) were taken on trotlines that were set in lakes or the slower-moving parts of rivers a few inches below the surface. I have records of only two *muticus* taken on trotlines. Goin (1948:304) stated that commercial fishermen catch softshells on trotlines set for catfish on the bottom of river beds. Evermann and Clark (1920:595) found softshells to be caught more often than any other kind of turtle in traps, on set lines, and by anglers in Lake Maxinkuckee, Indiana. Some residents of the South tell of so placing baits that turtles are lured to tread water against an object set with recurved hooks upon which the webbing of the forelimbs are impaled.

Individuals of *muticus* and *spinifer* frequently bury themselves in sand in shallow water and can be collected by hand by noting swirls or disturbances on the bottom caused by a turtle withdrawing its head (Conant, 1951:156, 159). Professional turtle collectors take them by "noodeling" (Conant, *op. cit.*:160); Lagler (1943a:22) elaborated on the method of "noodling." P. W. Smith (1947:39) remarked that 20 or more softshells were taken "within a few hours by probing sand bars at the water edge" near Charleston, Illinois. From a distance I observed an individual of *T. s. asper* bury itself in shallow water on the Escambia River, Florida. Small individuals of *muticus* have been taken by hand along the shore of Lake Texoma. Along the Flint River near Bainbridge, Georgia, two hatchlings that were buried in sand in shallow water emerged at my approach and scurried a few inches, then buried themselves again. Larger turtles seem to be more wary. One that was disturbed, emerged from the sand and swam toward deep water.

In clear water, water-goggling may be effective in securing softshells. Marchand (*in* Carr, 1952:417-18) mentioned that softshells (*ferox*) can be found buried in deep water with only the heads visible; the turtles are not easily frightened under water and may be captured by grasping their necks. A similar technique described by Allen and Neill (1950:3) resulted in the capture of trionychid turtles. In clear water of the White River, Arkansas, I collected a few softshells by hand as they lay on the bottom.

In shallow-water areas of large rivers, lakes and tributaries, seining often procures softshells. Methods used in fisheries investigations such as the application of rotenone and electric shockers, and even dynamiting, sometimes yield soft-shelled turtles. Carr (1952:419) wrote that numbers of *ferox* were incapacitated by rotenone in Florida lakes, although no other species of turtle was affected. I captured a snapping turtle (*Chelydra serpentina*) that was immobilized by the current from an electric shocker in a small, alga-choked tributary of Cache Creek, Comanche County, Oklahoma; presumably turtles must come in close contact with the electrodes to be affected (see discussion by Gunning and Lewis, 1957:52).

The effectiveness of gill nets in trapping turtles is indicated by information kindly supplied by Mr. Alfred Houser on gill-net operations from July through December, 1952, under the direction of Mr. "Bud" Oldham, a commercial fisherman. The 4-inch mesh nets were in Lake Texoma at the mouth of Briar Creek, two miles south of Powell, Marshall County, Oklahoma, in 25 to 30 feet of water. Eighty to 90 per cent of the turtles secured were softshells; more were taken near shoreline than away from shore even though the depth was about the same. An average of only one turtle every four days was taken in July and August when the turtles presumably are most active (Table 1). One gill-net day is equivalent to one gill net, 200 yards long, operated for 24 hours.

Dr. Virgil Dowell, while making fishery studies two miles east of Willis, Marshall County, Oklahoma, caught, on the average, 1.5 turtles per day. Of 75 turtles collected from July 1 through October 18, 1953, 66 were *Trionyx* (*spinifer* and *muticus*), five were *Graptemys* and four were *Pseudemys scripta.* No more than two gill nets were used simultaneously. The nets were moved from time to time and varied in dimensions, but those used most of the time were 200 feet long and eight feet deep with a 3-inch mesh.

TABLE 1. THE ABUNDANCE OF TURTLES AS REVEALED BY GILL-NET OPERATIONS IN LAKE TEXOMA, 1952.

MONTH	Gill-net days	Number of turtles	Gill-net days per turtle
July	835	213	3.9
August	816	199	4.6
September	743	42	17.7
October	1661	82	20.3
November	1322	48	27.5
December	864	5	172.8

The few captures by Houser probably resulted from long-continued trapping in one place; the gill nets were not moved in the entire six-month period or for some time previously. Breckenridge (1955:6) commented on the sedentary nature of *spinifer* (in Minnesota) and quoted a professional turtle trapper as stating that "after a section of a river has been trapped heavily for softshells, little success can be expected in that area for as much as three or four years thereafter." Both Houser's and Dowell's data indicate a higher percentage of soft-shelled turtles collected than any other species. The number caught probably depends, at least partly, on the food habits of the species and is influenced by the enmeshed fish, which, serving as a food source, attract the turtles.

Materials and Procedures

In the course of this study I examined 1849 soft-shelled turtles, including some incomplete alcoholic or dried specimens, such as those represented only by skulls or by other osteological material. Material was examined from each of the collections named below (except KKA), and these are mentioned in the text by the following abbreviations:

AMNH	American Museum of Natural History
ANSP	Academy of Natural Sciences, Philadelphia
BCB	Bryce C. Brown, private collection, Baylor University
CM	Carnegie Museum
CNHM	Chicago Natural History Museum
INHS	Illinois Natural History Survey, University of Illinois
KKA	Kraig K. Adler, private collection, data in letter dated January 8, 1960
KU	Museum of Natural History, The University of Kansas
LSU	Louisiana State University
MCZ	Museum of Comparative Zoology, Harvard College
MSU	The Museum, Michigan State University
NHB	Naturhistorisches Museum Basel, Switzerland
OU	University of Oklahoma Museum, Division of Zoology
SM	Strecker Museum, Baylor University
TCWC	Texas Cooperative Wildlife Collection, Texas Agricultural and Mechanical College
TNHC	Texas Natural History Collection, The University of Texas
TTC	Texas Technological College
TU	Tulane University
UA	University of Alabama
UI	Museum of Natural History, The University of Illinois
UMMZ	Museum of Zoology, The University of Michigan
USNM	United States National Museum
WEB	William E. Brode, private collection, Mississippi Southern College
WTN	Wilfred T. Neill, private collection

External measurements (listed under the section, "Variation") were taken by the writer by means of a Vernier caliper or a steel tape. Measurements of the skulls are in millimeters and tenths as taken by the writer with dial calipers. Partial wrinkling of the carapace at the edges of some specimens causes some error in measurements; consequently, length of plastron is used as the measurement of reference.

Scattergrams based on external measurements were constructed. Some demonstrate considerable ontogenetic variation. An inspection of the scattergrams indicated regressions essentially linear in nature, but sometimes occasioned an arbitrary separation of samples into size groups to show ontogenetic variation; no secondary sexual differences could be discerned. Several ratios were developed from the measurements. The data correspond to the regression model 1A in "Statistical Methods" (Snedecor, 1956, sec. 6.13); consequently, the sample ratios indicate the slope of regression and are useful in comparisons. Sample-means and their estimated standard errors are compared graphically to show general trends in proportional characters. Comparisons of means and standard errors indicate statistical significance between populations if the sample-means plus or minus twice their standard errors do not overlap, but this method of comparison is valid only when comparing two samples (Pimentel, 1959:100).

In the section on "Variation," general features applicable to all kinds of soft-shelled turtles are discussed under the following headings: secondary sexual, ontogenetic, and geographic; individual variation is mentioned in accounts of species and subspecies. In the section "Character Analysis" external and osteological characters having taxonomic significance are discussed.

Vernacular names follow, as closely as possible, those recommended by the Committee on Herpetological Common Names (1956). The synonymy of each monotypic species or subspecies begins with the name as given in the original description. The second entry is the name-combination herein applied to the taxon. Other entries are first usages, in chronological order, of other names (synonyms) that have been applied to the taxon in question. Next, the type is briefly discussed followed by the "Range" defined in general geographic terms, and, when appropriate, in terms of river drainage systems. "Diagnosis" includes a combination of characters that facilitates quick identification. In polytypic species, the diagnosis of a subspecies is designed only to distinguish it from other subspecies of that species. The comments included under the subsection entitled "Description" pertain to individuals from an area where the taxon is most clearly differentiated. Because osteological characters are significant only at the specific level, they appear under the accounts of each species (excluding *ater*). Proportional characters as given in the "Diagnosis" are only in general terms; more specific data are set forth in the subsection, "Description" or in the various text figures, mostly in the section on "Variation," page 445. Proportions pertaining to the species *muticus* were derived only from the nominal subspecies, and appear under the account of the species. A subsection "Variation" under the accounts of some subspecies includes information concerning principally individual variation and coloration; because color is not considered to be of major taxonomic importance, color terms are used without reference to any standard color guide. The subsection "Remarks" follows the section on "Comparisons," and may include comments on nomenclature, intergradation and other information related to the distribution or taxonomy of the subspecies.

The probable geographic range of each species and subspecies is shown on one of the maps. Locality records of specimens that I have examined are shown by solid circles. Additional records of occurrence (published records or specimens otherwise not seen) are shown by hollow circles. Localities only a short distance apart share the same circle.

Under the subsection "Specimens examined," a number in parentheses following a museum number indicates the number of specimens referable to that museum number. All localities of specimens examined are indicated on one of the maps. The list of specimens is arranged alphabetically by states (Canadian provinces precede states of the United States under the account of *T. spinifer spinifer,* and Mexican states follow those of the United States under *T. s. emoryi*), alphabetically by counties, and within a county alphabetically by abbreviations of museums; then, museum catalogue numbers are arranged consecutively. Records in the literature are not included if they refer to the same locality from which at least one specimen has been examined, or refer to a less restricted locality that includes the area from which at least one specimen has been examined. Localities within a county are arranged alphabetically by author; the appropriate reference may follow several localities.

All generic, specific and subspecific names (but not all the different kinds of name-combinations) that have been applied to American soft-shelled turtles are listed in a subsection entitled "Synonymy" under the heading "Genus Trionyx Geoffroy, 1809."

Acknowledgments

Completion of this study has been made possible only by the co-operation of those persons in charge of the collections listed above and I am grateful to them for the privilege of examining specimens. Also I wish to thank Dr. E. Raymond Hall for the facilities afforded by the Museum of Natural History at the University of Kansas, as well as for editorial assistance in the preparation of the manuscript, and especially Dr. Henry S. Fitch under whose guidance this research was carried out.

In addition to various staff members, graduate students, and individuals whose help is acknowledged at appropriate places in the text, Dr. Rollin H. Baker, Dr. Fred R. Cagle, Mr. J. Keever Greer, Dr. A. Byron Leonard, Dr. Carl D. Riggs, and Dr. Edward H. Taylor deserve especial mention for aid extended in the course of this study. I am indebted to Mr. J. C. Battersby, British Museum (Natural History), London, for information concerning the type of *Trionyx ferox*, to Dr. Jean Guibé, Museum d'Histoire Naturelle, Paris, for information concerning the types of *Trionyx muticus*, *T. spinifer* and *T. carinatus*, and photographs of the types of *T. muticus*, *T. spinifer* and *T. ocellatus*, and to Dr. Lothar Forcart of the Naturhistorisches Museum, Basel, Switzerland, for information pertaining to a published record of *T. muticus*.

The maps and figures are the work of Miss Lucy Jean Remple and Mrs. Lorna Cordonnier, University of Kansas. Dr. John M. Legler, University of Utah, prepared most of the photographs on plates 1-20; photographs as mentioned in the preceding paragraph were received from Dr. Guibé, one was provided through the co-operation of Roger Conant and Isabelle Hunt Conant, another was furnished by Mr. J. Keever Greer, and the others were taken by me. Field work was financed in part by funds provided by the Sigma Xi-RESA Research Fund.

TAXONOMY

Family Trionychidae Bell, 1828

Recent soft-shelled turtles comprise a well-defined assemblage of the family Trionychidae. Although the scope of this study does not involve an assay of the relationships of the soft-shelled turtles of the Old World, a brief résumé that includes some of the salient characteristics of the family is included.

Diagnosis.—Articulation between last cervical and first dorsal vertebrae by zygopophyses only; preplastra separated from hyoplastra by Λ-shaped epiplastron, entoplastron absent (Williams and McDowell, 1952:263-75); marginal bones absent or forming an incomplete series, not connected with ribs that extend beyond pleural plates; claws on only three inner digits; fourth digit having four or more phalanges; plastron united to carapace by ligamentous tissue (Smith, 1931:147).

General characters.—Size large, ". . . some attaining probably 5 feet in length of carapace" (Boulenger, 1890:10); body depressed; carapace and plastron lacking horny epidermal shields, covered instead with soft skin; snout ending in fleshy, tubate proboscis; jaws concealed by fleshy lips; tail short; digits well-webbed; cervical vertebrae opisthocoelous (eighth having double articulation in front); neck elongate, cervical region equalling or exceeding length of dorsal vertebral column; head and neck completely retractile, bending by means of sigmoid curve in vertical plane; ear hidden; skull elongate, having three posterior projections (median one produced by supraoccipital and two lateral projections formed chiefly by squamosals); temporal region emarginate posteriorly, forming wide shallow fossa; premaxillae fused; an intermaxillary foramen; pterygoids separated by basisphenoid that contacts palatines; vomer, if present, not separating palatines; pelvis not fused to carapace and plastron; plastron reduced, a median vacuity usually present; plastral bones developing sculpturing with increase in size, forming four to seven so-called plastral callosities; carapace with or without prenuchal bone; nuchal overlapping or overlapped by first pleural; neurals in continuous series or interrupted by pleurals; bony plates of carapace sculptured; mandible having well-developed coronoid bone; cutaneous femoral valves that conceal hind limbs present or absent; two or three pairs of scent glands; cloacal bursae absent (Smith and James, 1958: 89); forelimbs having antebrachial scalation; body of hyoid apparatus formed of two or three pairs of bones; penis broad, expanded and pentifid, sulcus spermaticus quadrifid having branches in each of four lateral projections (Hoffman, 1890:298, pl. 47, fig. 2); aquatic, principally in fresh water; mainly carnivorous; flesh of many species eaten. (See Boulenger, 1889:237-41; Loveridge and Williams, 1957:412; Romer, 1956:513; Smith, *op. cit.*:147-54).

Recent distribution (Figure 1).—North America, from extreme southeastern Canada and eastern United States west to Rocky Mountains and south to northern México; introduced in southwestern United States (Conant, 1958: 69-73). Africa, from Egypt and Senegal south to Angola and Zambesi River drainage (Loveridge and Williams, *op. cit.*:412-68); occurrence of *Trionyx triunguis* in Syria (Boulenger, *op. cit.*:255) and coastal streams of Palestine (Schmidt and Inger, 1957:36) considered accidental by Flower (1933:753-54). Southwestern Asia (Tigris and Euphrates River drainage) in eastern Turkey, Syria, Iraq and northeastern Israel (Mertens and Wermuth, 1955:388). Southeastern Asia, from Pakistan and India (Indus River drainage) and Manchuria and adjacent Siberia (Amur River drainage) to Ceylon, Japan, Formosa, Hainan, Luzon, Sumatra, Java, Borneo, Timor and southeastern New Guinea (De Rooij, 1915:325-32; Okada, 1938:108; Pope, 1935:60-64; Smith, 1931: 158-79; Stejneger, 1907:514-532; Taylor, 1920:141).

Trionyx cartilagineus is questionably recorded from the Moluccas (De Rooij, *op. cit.*:330). *T. sinensis* has been introduced on Kauai Island, Hawaiian Islands (Brock, 1947:142; Oliver and Shaw, 1953:83), one of the Bonin Islands (Okada, 1930:187-94), and probably Timor (De Rooij, *op. cit.*:331). All insular records east of Borneo and Java are probably the result of introductions,

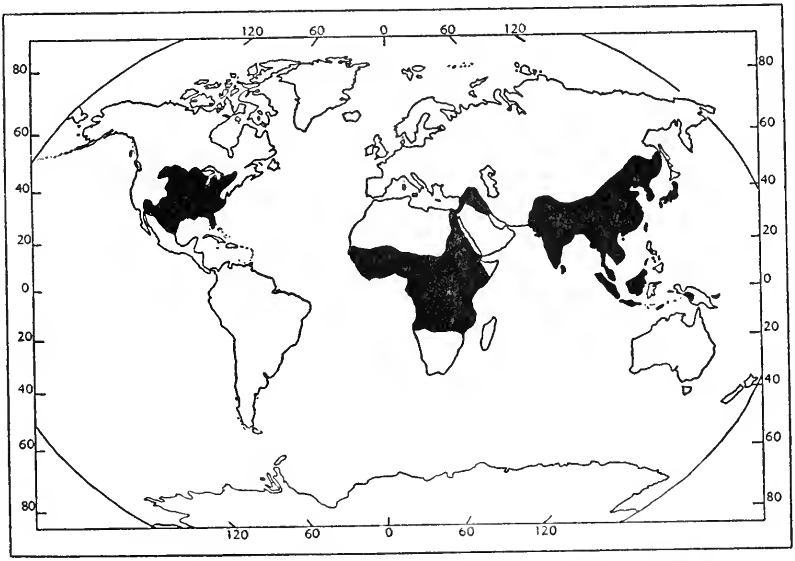

FIG. 1. Geographic distribution of the family Trionychidae.

except perhaps those of *Pelochelys* on Luzon and New Guinea (Darlington, 1957:210).

Recent genera.—According to Mertens and Wermuth (1955:387-95), there are 21 species belonging to six genera as follows:

Chitra Gray, 1844 (1)	*Lissemys* Smith, 1931 (1)
Cyclanorbis Gray, 1854 (2)	*Pelochelys* Gray, 1864 (1)
Cycloderma Peters, 1854 (2)	*Trionyx* Geoffroy, 1809 (14)

Dogania is considered a synonym of *Trionyx* (Loveridge and Williams, *op. cit.*:422).

Geologic range.—Lower Cretaceous (possibly Upper Jurassic) to Recent of Asia; Upper Cretaceous to Recent of North America; Paleocene (Upper Jurassic, assuming *Trionyx primoevus* is a trionychid) to Pleistocene of Europe; Lower Miocene to Recent of Africa; Pleistocene to Recent in East Indies (Loveridge and Williams, *op. cit.*:412; Romer, 1945:594); questionable trionychid fragments from Pleistocene of Australia (Darlington, *loc. cit.*).

Remarks.—The genera *Lissemys, Cyclanorbis* and *Cycloderma* are distinguished from *Pelochelys, Chitra* and *Trionyx* by several characters (Loveridge and Williams, *op. cit.*:414). The recognition of two groups of genera caused Deraniyagala (1939:290) to erect two families, Cyclanorbidae and Trionychidae. An appraisal of fossils prompted Hummel (1929:768) to propose two corresponding subfamilies, Cyclanorbinae and Trionychinae. Williams (1950:554) considered the two groups as subfamilies (Lissemydinae and Trionychinae).

Baur (1887:97) regarded the Trionychidae as constituting a separate suborder distinct from the rest of the living turtles. Later (1891), however, he pointed out the resemblances of the Trionychidae and Carettochelyidae (having one living genus in New Guinea), and the cryptodiran affinities of *Carettochelys.* Bergounioux (1932:1408) mentioned the close resemblance of the Carettochelyidae to *Trionyx* but considered the former as having pleurodiran affinities, a view adopted by Deraniyagala (*loc. cit.*). Most students now consider the two families to be closely related, and conceive of both as members of the suborder Cryptodira (Hummel, 1929:768; Williams, *loc. cit.;* Mertens and Wermuth, 1955).

The oldest trionychid fossil, *Trionyx primoevus,* is from marine deposits of the Upper Jurassic (Kiméridgien) from "Cap de la Hève," and its characters do not indicate the kind of cryptodiran ancestor from which the family arose (Bergounioux, *op. cit.*:1409; 1937:188). Lane (1910:350) found that the entoplastron (= epiplastron) was paired in embryos of *Trionyx* and regarded that genus as the most primitive of the order; he also mentioned Wiedersheim's report of rudiments of teeth in embryos of *Trionyx.* Baur (1891:637-38) thought that the family arose directly from the Amphichelydia, that the ancestors of the Trionychidae closely resembled *Carettochelys* in the structure of the carapace and plastron, and that a progressive reduction in ossification of those structures occurred. Nopcsa (1926:654) also wrote that the family originated from ancestors having a well-developed plastron; he maintained that the progressive reduction in ossification of the plastron was a specialization for aquatic life, and that the more primitive trionychids had the best developed bones and callosities. Hummel (1929:772) also thought that there had been a progressive reduction in ossification. Bergounioux (1932:1408; 1936:1088, 1952: 2304), on the contrary, thought that there had been a progressive increase in ossification of the marginal bones in both families as well as of the plastron (1936:1088; 1937:190). Zangerl's study of the shell elements of turtles (1939:393) indicated that *Trionyx* was highly specialized in having a well-developed epithecal armor (sculptured callosities, neurals and costals), and that it occurred in most aquatic turtles; the development in soft-shells suggested that members of the family had maintained an aquatic mode of life over a long period of geologic time, a view supported by Deraniyagala (1930:1066). Of interest are Stunkard's remarks (1930: 214-18) concerning several *Trionyx spinifer* that were obtained from a commercial supply house and found to be infested with pronocephalid trematodes (*Opisthoporus* [= *Teloporia*] *aspidonectes*). The closest relatives of that trematode (also recorded from *T. ferox*) live in marine turtles. Possibly, a Mesozoic ancestor of marine and essentially fresh-water soft-shelled turtles harboured ancestors of these trematodes, but possibly the parasites may have transferred relatively recently to their present hosts. Bergounioux (1937:190) judged the Trionychidae to be an ancient group of marine origin. Hummel (1929:770) wrote that the Trionychidae originated in east Asia (the region of most differentiation) in humid climates.

Baur (1891:634, 637) pointed out that the dorsal aspect of the skull of the closely related *Carettochelys* resembles the skull of the Dermatemydidae, Staurotypidae and Kinosternidae; the close relationship of *Carettochelys* and the Dermatemydidae is also mentioned by Bergounioux (1952:2304) and Hummel (1929:769). Hummel (*op. cit.*:771) thought that the Carettochelyidae and "die Chelydroiden" had a common ancestor, and that (*op. cit.*:772) the origin of the Trionychidae was older than those two groups. Dunn (1931:109) wrote that the Kinosternidae, Carettochelyidae and Dermatemydidae represented the same general ancestry. Williams (1950:552) has shown the resemblance of the cervical articulations in members of the Chelydridae (including Staurotypinae and Kinosterninae) and the Central American family Dermatemydidae. The consensus of opinion, then, is that the families Trionychidae, Carettochelyidae, Chelydridae and Dermatemydidae are relatively closely related.

Genus Trionyx Geoffroy, 1809

Testudo Linnaeus (in part), Syst. Nat., Ed. 10, 1:197, 1758; type, *Testudo graeca* Linnaeus by subsequent designation (Fitzinger, 1843:29).

Trionyx Geoffroy, Ann. Mus. Hist. Nat. Paris, 14:1, August, 1809; type, *Trionyx aegyptiacus* (= *Testudo triunguis* Forskål) by original designation.

Apalone Rafinesque, Atlan. Jour., Friend of Knowledge, Philadelphia, 1 (No. 2, Art. 12):64, Summer, 1832; type, *Apalone hudsonica* (= *Trionyx spiniferus* Lesueur) by monotypy.

Mesodeca Rafinesque, Atlan. Jour., Friend of Knowledge, Philadelphia, 1 (No. 2, Art. 12):64, Summer, 1832; type *Mesodeca bartrami* (= *Testudo ferox* Schneider) by monotypy.

Aspidonectes Wagler, Naturl. Syst. Amphib., p. 134, 1830; type, *Aspidonectes aegyptiacus* Wagler (= *Testudo triunguis* Forskål) by subsequent designation (Fitzinger, 1843:30).

Amyda Fitzinger, Ann. Wiener Mus. Naturg., 1:110, 120, 127, 1835; type, *Amyda subplana* Fitzinger by subsequent designation (Fitzinger 1843:30).

Gymnopus Duméril and Bibron, Erpét. Gén., 2:472, 1835; new (substitute) name for *Aspidonectes* Wagler.

Pelodiscus Fitzinger, Ann. Wiener Mus. Naturg., 1:110, 120, 127, 1835; type, *Pelodiscus sinensis* Fitzinger by subsequent designation (Fitzinger, 1843:30).

Platypeltis Fitzinger, Ann. Wiener Mus. Naturg., 1:109, 120, 127, 1835; type, *Platypeltis ferox* by subsequent designation (Fitzinger, 1843:30).

Potamochelys Fitzinger, Syst. Rept., p. 30, 1843; type, *Aspidonectes javanicus* Wagler (= *Testudo cartilaginea* Boddaert) by original designation.

Tyrse Gray, Cat. Tort. Croc. Amphis. Brit. Mus., p. 48, 1844; type, *Tyrse nilotica* Gray (= *Testudo triunguis* Forskål) by tautonomy (*Tyrse,* a name for the Nile River).

Callinia Gray, Proc. Zool. Soc. London, p. 222, 1869; new (substitute) name for *Aspidonectes* of Agassiz (1857:403); type, *Callinia spicifera* (mispelling for *spinifera*) Gray by subsequent designation (Stejneger, 1907:514).

Euamyda Stejneger, Bull. Mus. Comp. Zool., 94:7, 9, 12, 1944; new (substitute) name for *Amyda mutica* of Agassiz (1857:399); type, *Amyda mutica* Agassiz by monotypy.

Type Species.—*Trionyx aegyptiacus* (= *Testudo triunguis* Forskål).

Diagnosis.—Cutaneous femoral valves absent; width of postorbital arch of skull less than diameter of orbit; pterygoids usually not contacting opisthotics; carapace lacking prenuchal bone and marginal ossifications; nuchal bone lacking conspicuous ventral ridges; posterior margin of nuchal overlying first pair of pleurals; lateral parts of nuchal bone overlying second pair of ribs; neurals seven or eight, rarely six or nine; pleurals seven or eight pairs, posterior one or two pairs sometimes in contact medially; distinct suture usually present between hyoplastra and hypoplastra; most laterad prong of posteromedial process of hypoplastra inserted between bifid anterolateral process of xiphiplastra.

Synonomy.—Geoffroy published a synopsis of the species he recognized (1809) prior to his formal description of the genus *Trionyx* (1809a). Schweigger, nevertheless, probably was the first person to recognize the soft-shelled turtles as a distinct group, and he proposed for it the name *Amyda* in an unpublished manuscript that he sent to Geoffroy. The latter author (1809a:15) relegated the name *Amyda* to the synonomy of *Trionyx javanicus* by means of the following entry: "*Amyda javanica.* Schweigger, dans un manuscript communique a l'Institut." Stejneger (1944:7) maintained that this publication of Schweigger's monotypic generic name clearly established its availability for the species congeneric with *Amyda javanica* (= *Testudo cartilaginea* Boddaert, 1770). Loveridge and Williams (1957:422) contend that this mere mention of the name *Amyda* neither constitutes the proposal of a new name nor validates it, and that the first valid usage of the name *Amyda* is that of Fitzinger (1835:120), who later (1843:30) designated the type species as *Amyda subplana.* The name *Amyda* cannot date from *Oken* (1816:348) as Volume 3 [Zoologie] of his Lehrbuch der Naturgeschichte published in 1815-1816 has been placed on the Official Index of Rejected and Invalid Works in Zoological Nomenclature with the Title No. 33; see Opinion 417 (Hemming, 1956).

There has been considerable debate as to whether Geoffroy did or did not designate a type species of the genus *Trionyx* (1809a). Although not specifically designated as the type species, *Trionyx aegyptiacus* (= *Testudo triunguis* Forskål) is considered by Smith (1930:2), Schmidt (1953:108, footnote), and Loveridge and Williams (1957:422) to have been sufficiently indicated by Geoffroy as the type species. But Stejneger (1944:6), H. M.

Smith (1947:122), Conant and Goin (1948:11), and Mertens and Wermuth (1955) maintained that Geoffroy did not adequately designate a type species, and that Fitzinger (1843:30) designated the type species as *Trionyx granosus* (= *Lissemys punctata*), a synonym of Geoffroy's species, *coromandelicus*.

If Fitzinger's designation of a type species is accepted, the name *Trionyx* is applicable to the forms herein referred to *Lissemys*, and *Amyda* to the American forms. If Geoffroy's designation is accepted, the American forms are referable to *Trionyx*, and *Amyda* is a synonym.

The preceding includes only those generic names (listed in chronological order) that have been applied to Recent American soft-shelled turtles. Generic synonyms of the genus *Trionyx* applicable to Old World species are listed by Stejneger (1907:514), Smith (1931:165), and Loveridge and Williams (1957:420-21).

Trionyx is the most widespread genus of the family; most of the species occur in southeastern Asia. All North American soft-shelled turtles belong to this genus.

For quick reference, all the specific and subspecific names proposed for soft-shelled turtles in North America are listed below in alphabetical order (left hand column) with their nomenclatural status as recognized in this paper. The synonyms are listed in the account of the appropriate species or subspecies, and are discussed under the subsection entitled "Remarks."

agassizi	*Trionyx*	*spinifer asper*
annulifer	*Trionyx*	*spinifer spinifer*
argus	*Trionyx*	*spinifer spinifer*
asper	*Trionyx*	*spinifer asper*
ater	*Trionyx*	*ater*
bartrami	*Trionyx*	*ferox*
emoryi	*Trionyx*	*spinifer emoryi*
calvatus	*Trionyx*	*muticus calvatus*
ferox	*Trionyx*	*ferox*
georgianus	*Trionyx*	*ferox*
georgicus	*Trionyx*	*ferox*
harlani	*Trionyx*	*ferox*
hartwegi	*Trionyx*	*spinifer hartwegi*
hudsonica	*Trionyx*	*spinifer spinifer*
mollis	*Trionyx*	*ferox*
microcephalus	*Trionyx*	*muticus muticus*
muticus	*Trionyx*	*muticus muticus*
nuchalis	*Trionyx*	*spinifer spinifer*
ocellatus	*Trionyx*	*spinifer spinifer*
olivaceus	*Trionyx*	*spinifer spinifer*
spiniferus	*Trionyx*	*spinifer spinifer*

Variation

Aside from qualitative variations and comparisons of patterns of pigmentation the following external measurements (to the nearest millimeter) were used.

Length of plastron: Maximal straight-line measurement (midventrally), from the anteriormost region of the ventral surface to the posterior end of the plastron; this measurement includes an anterior cartilaginous part.

Length of carapace: Maximal, straight-line measurement (middorsally), from the nuchal region to the posteriormost region of the free edge of the carapace.

Width of carapace: Maximal, straight-line measurement between the lateral margins of the carapace.

Plane of greatest width of carapace: Maximal, straight-line measurement from the posteriormost region of the free edge of the carapace to a point on the middorsal line at the level or plane of the greatest width of the carapace; this measurement and the last two, of course, include the fringing cartilaginous parts of the dorsal bony carapace.

Width of head: Maximal measurement between the lateral margins of the head.

Length of snout: Measurement from tip of snout to interorbital region of least breadth.

Diameter of ocellus: Maximal outside diameter of largest (not conspicuously ovoid or oblong) ocellus on carapace.

The following ratios were developed from the measurements. Reference to these ratios will be made by the abbreviations within the parentheses: length of carapace/length of plastron (CL/PL); length of carapace/width of carapace (CL/CW); length of carapace/plane of width of carapace (CL/PCW); length of plastron/width of head (PL/HW); width of head/length of snout (HW/SL); diameter of ocellus/length of plastron (OD/PL).

Secondary Sexual Variation

Size

In many species of turtles, females are larger than males; the difference in size between the sexes is probably most pronounced in aquatic emydids. The ten largest individuals of each sex were selected to indicate the relative difference in size between the sexes of the three American species of *Trionyx* (excluding *ater*, Table 2). Female soft-shelled turtles attain a larger size than males. *T. ferox* is the largest species; *muticus* is the smallest. The approximate maximal size of each sex and the difference in size between the sexes are more correctly expressed for *spinifer* and *muticus* than for *ferox*, because fewer specimens of *ferox* were examined; presumably the approximate maximal size of males and females of *ferox* is larger than is indicated in Table 2.

TABLE 2. SECONDARY SEXUAL DIFFERENCE IN MAXIMAL SIZE OF NORTH AMERICAN SPECIES OF THE GENUS TRIONYX (EXCLUDING ATER) BASED ON THE TEN LARGEST SPECIMENS OF EACH SEX OF EACH SPECIES. THE EXTREMES PRECEDE THE MEAN (IN PARENTHESES).

SPECIES	Plastral length (cm.)	
ferox	males	17.0–26.0 (20.0)
	females	23.3–34.0 (27.9)
spinifer	males	13.8–16.0 (14.4)
	females	26.0–31.0 (28.0)
muticus	males	11.8–14.0 (12.3)
	females	17.7–21.5 (18.9)

Pattern

Secondary sexual differences in pattern are probably more pronounced in soft-shelled turtles than in other species of turtles, except perhaps for the well-known melanism and concomitant obliteration of pattern acquired by some adult males of the *scripta* section of the genus *Pseudemys*.

The difference in pattern between the sexes of American species varies with size of the individual and with the species and subspecies. The juvenal pattern of some individuals of *T. spinifer asper* differs according to sex. In the other species and subspecies, there are no secondary sexual differences in the juvenal pattern. That pattern in females of all species and subspecies is partly or entirely obscured by a mottled and blotched pattern as growth proceeds. This mottled and blotched pattern is present on females not yet sexually mature, and is of contrasting lichenlike figures, and in other individuals is less contrasting and a more uniform coloration. The largest males of *T. spinifer* retain a conspicuous juvenal pattern; in those of *muticus* the pattern may be well-defined or partly modified and obscured, whereas in large males of *ferox* the juvenal pattern is ill-defined or absent. No male normally acquires a contrasting mottled and blotched pattern on the carapace. The pattern on the carapace of many large individuals of *ferox* is not distinctive as to sex.

On the dorsal surface of the soft parts of the body there is a contrasting pattern in adult males and hatchlings of some forms, but in most large females the pattern is usually reduced to a near-uniform coloration; the pattern on adult males of *ferox* and *muticus* is not contrasting and resembles that on large females.

Coloration

Because most specimens examined were preserved, the detection of secondary sexual differences in coloration was difficult. There is one difference in coloration between the sexes in the subspecies *T. s. emoryi*. Males from the Río Grande drainage, at least those from the Big Bend region of Texas, and southwestward in the Río Conchos into Chihuahua, México, are bright orange on the side of head (postlabial and postocular pale areas); an orange tinge also occurs in pale stripes on the snout, and pale orange blotches sometimes occur on the dorsal surfaces of limbs, especially the hind limbs. The coloration of these areas on females is pale yellow, lacking orange.

Tuberculation

In all subspecies of *spinifer* the carapace of adult males is "sandpapery" owing to abundant, small, spiny tubercles distributed over its surface; all females lack spiny tubercles on the surface of the carapace.

Length of Tail

Elongation of the preanal region of the tail resulting in the extension of the cloacal opening beyond the posterior edge of the carapace occurs in males of several kinds of turtles, including *Trionyx*, at least in those from Louisiana, Texas, and Lake Texoma, Oklahoma (Webb, 1956:121). Probably this elongation is characteristic of males of all American softshells. Some females of *spinifer* and *muticus* that exceed the maximum size attained by males have the tip of the tail and cloacal opening extending a short distance beyond the posterior edge of the carapace. Some large females of *ferox* have more elongate tails than those of *spinifer* and *muticus*.

Width of Alveolar Surfaces of Jaws

Stejneger (1944:34-36, pl. 6) commented on a series of large skulls of *ferox* mostly from Kissimmee, Florida, some of which had conspicuously expanded alveolar surfaces. He suggested that the condition was confined to large males. A scattergram (Fig. 2) based on measurements obtained from 45 skulls of *ferox* shows widened alveolar surfaces of the upper jaws on some of the larger skulls. Because the maximal size of adult males is unknown and the difference in size between the sexes of *ferox* is slight, such large skulls might represent either sex. The sex had been recorded for only three of the 45 skulls; none of the three exceeded 82 millimeters in basicranial length or had widened alveolar surfaces. Some of the larger skulls of approximately the same size differ markedly in width of the alveolar surfaces; this difference suggests that both sexes are included and that the sexes may be of approximately the same maximal size. On the other hand, the variation observed in skulls is possibly confined to one sex. To judge from what is known of the maximal sizes of the sexes of *spinifer* and *muticus* (see Table 2), skulls of *ferox* of more than 85 millimeters in basicranial length probably are of females. The largest alcoholic male (dissected) of *ferox* that I examined had a width of head of approximately 46.5 millimeters; that measurement corresponds to a basicranial length of 70 to 75 millimeters. The specimen of which measurements are depicted by the uppermost symbol in the scattergram (represented by KU 16528) was recorded as a female. Large females of *T. s. asper* from rivers emptying into the Atlantic Ocean have broadened alveolar surfaces.

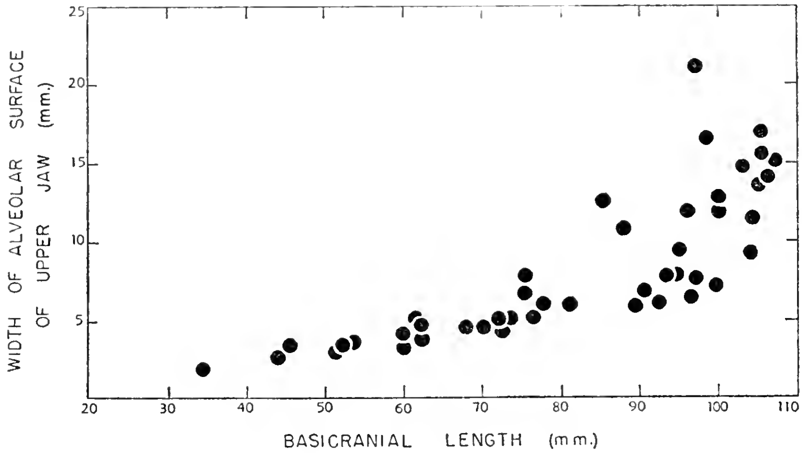

FIG. 2. Basicranial length and greatest width of alveolar surface of upper jaw on 45 skulls of *T. ferox*. Some skulls (sex unknown) in which the basicranial length exceeds 85 mm. develop widened alveolar surfaces of the jaws.

Length of Claw

Secondary sexual differences in length of claw on the forelimb are pronounced in some kinds of turtles. Cahn (1937:178) stated that the female of *Trionyx muticus* usually has long claws on the hind feet, while the male has long claws on the forefeet, but I am unable to substantiate his statement. Measurements of length of the third claw on the hind limb taken in 41 males and 45 females of *spinifer* from Louisiana showed no secondary sexual difference.

Ontogenetic Variation

Pattern

In all species and subspecies the juvenal pattern is replaced in females as growth proceeds by a mottled and blotched pattern that is contrasting or of nearly uniform coloration. The blotched pattern (of lichenlike figures) is evident on the carapaces of most females that have plastra so long as 8.0 centimeters. The contrasting juvenal pattern on the dorsal surfaces of the soft parts of the body is correspondingly modified in females, but at a size larger than 8.0 centimeters. Size of ocelli (OD/PL) in *T. s. spinifer* and *hartwegi* seems to vary ontogenetically (see section on Geographic Variation).

Some hatchlings have blotched patterns (*T. spinifer asper*, TU 16689.2, plastral length, 3.5 cm.); the largest females examined that did not show any evidence of mottling were two *asper* having plastrons 7.6 and 8.0 centimeters in length. Variation in color and pattern probably is modified greatly by the environment (Heude *in* Stejneger, 1907:518, footnote d) and the physiological condition of the individual. Smith, Nixon and Minton (1949:92) reported that a female of *T. s. hartwegi* developed a striking melanistic pattern in captivity and they concluded that patterns of soft-shelled turtles may be produced not only by conventional chromatophores, but also by other depositions, both intra- and extracellular. TU 16170, taken from brackish water at Delacroix Island, St. Bernard Parish, Louisiana, is the only adult male I have seen that had a blotched pattern (orange-brown in life) on the carapace in addition to the juvenal pattern. One female of *muticus*, KU 48229, having a plastral length 14.5 centimeters, retained a well-defined juvenal pattern, and lacked a mottled and blotched pattern (see Pl. 46).

Tuberculation

Males of the subspecies of *spinifer* develop small, sharp tubercles on the dorsal surface of the carapace when sexually mature. As growth proceeds, the minute prominences along the anterior edge of the carapace on hatchlings of both sexes of *spinifer* change in shape to conical projections or low, flattened, scarcely-elevated prominences, depending on the subspecies (Fig. 8).

Large females of *spinifer* and *ferox* acquire enlarged, flattened knobs in the nuchal region and posteriorly in the center of the carapace.

Length of Tail

The preanal region of the tail rapidly elongates in males of all soft-shells when they are sexually mature.

Width of Alveolar Surfaces of Jaws

The alveolar surfaces of the jaws are conspicuously broadened in large adults of *ferox*, and females of that population of *T. s. asper* in the Atlantic Coast drainage.

Ratios

Width of head increases at a rate slightly slower than does the length of the plastron (PL/HW, Fig. 3). The change in proportions is most pronounced

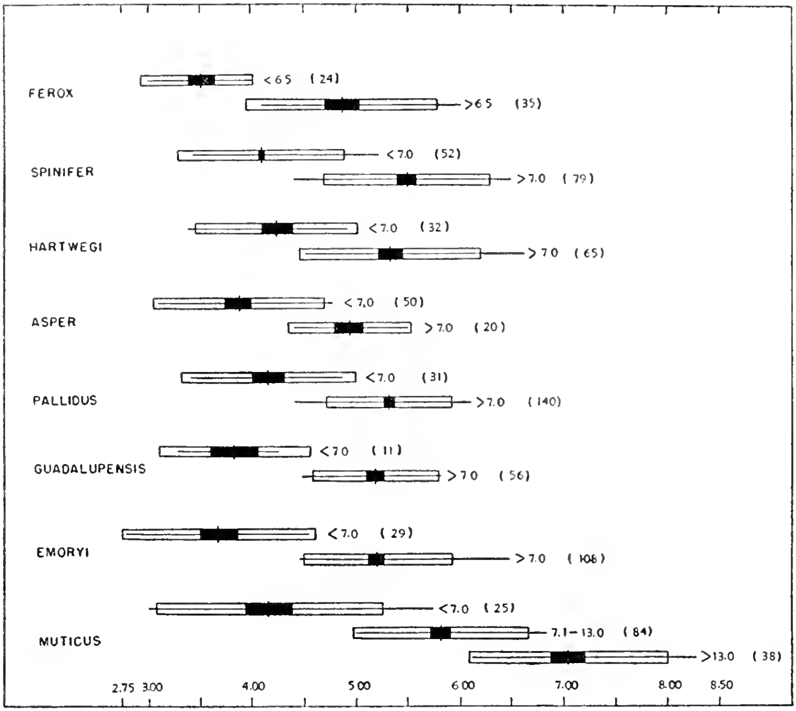

Fig. 3. Ratio of length of plastron to width of head (PL/HW) in some American species and subspecies of the genus *Trionyx*. The size of each sample is given in parentheses following an indication of the range (< = less than, > = greater than) in length of plastron (in cm.) of each sample. The horizontal line indicates the observed variation; the vertical line, the mean; the white rectangle, four standard deviations; and the black rectangle, four standard errors of the mean. There is some ontogenetic variation in PL/HW. The head is narrowest in *muticus* and widest in *ferox*.

at a plastral length of 7.5 to 8.0 centimeters. In general, the head is narrowest in *muticus* and widest in *ferox*. *T. s. asper* and *emoryi* seemingly have the widest heads among the subspecies of *spinifer*. Geographically width of head increases from *spinifer* and *hartwegi* through *pallidus* and *guadalupensis* to *emoryi*. *T. ater* terminates the cline; 12 specimens, ranging in plastral length from 9.6 to 18.4 centimeters, resemble *ferox* and *asper* in having wide heads (average PL/HW of 4.93).

The carapace increases in width more slowly than it increases in length (CL/CW, Fig. 4). The change in proportions is most pronounced when the carapace is 8.0 to 8.5 centimeters in length. Ontogenetically *muticus* varies least and *ferox* most; large specimens of *ferox* have narrower carapaces than *muticus* of corresponding size. There is also an indication of a geographical gradient that parallels the cline mentioned above for PL/HW. There is a gradual decrease in width of carapace from *pallidus* through *guadalupensis* to *emoryi*. Of the subspecies of *spinifer*, *emoryi* has the narrowest carapace and resembles *ferox*. In *T. ater* this cline is accentuated and terminates; 12 specimens, ranging in plastral length from 9.6 to 18.4 centimeters, resemble *ferox* and *emoryi* in having narrow carapaces (average CL/CW of 1.32).

Osteological Characters

Closure of the anterior, paravertebral fontanelles on the bony carapace, and size and number of plastral callosities are subject to ontogenetic variation (see sections entitled "Carapace" and "Plastron").

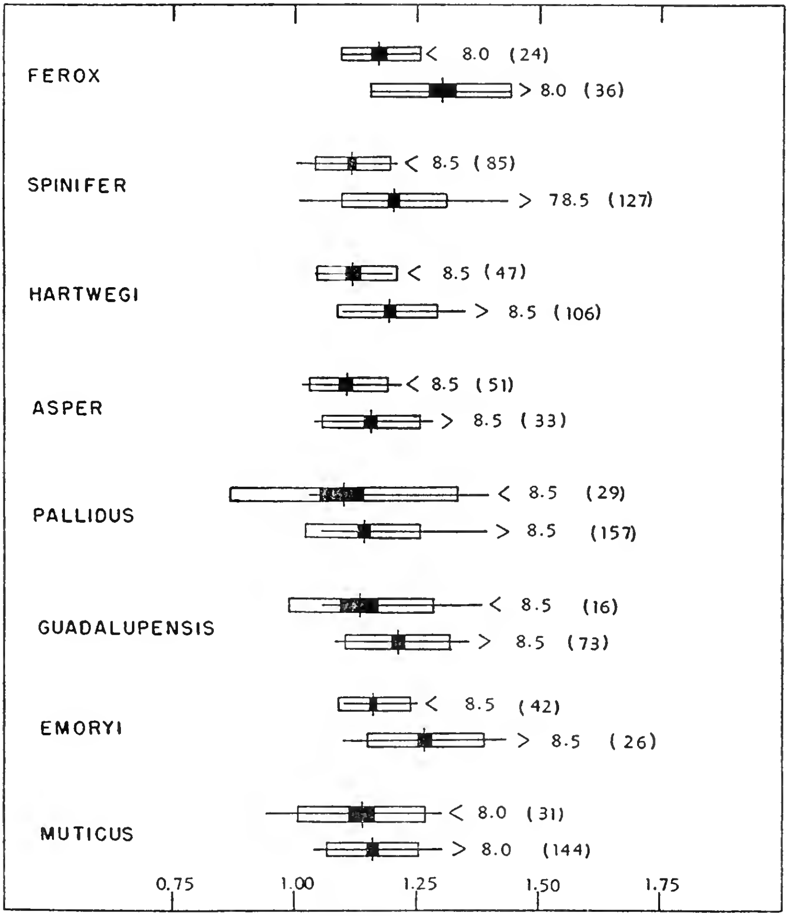

Fig. 4. Ratio of length of carapace to width of carapace (CL/CW) in some American species and subspecies of the genus *Trionyx*. Symbols as in Fig. 3. There is some ontogenetic variation in CL/CW (least in *muticus*). The carapace is narrowest in *ferox* and *emoryi*, and widest in *muticus*, *pallidus* and *asper*.

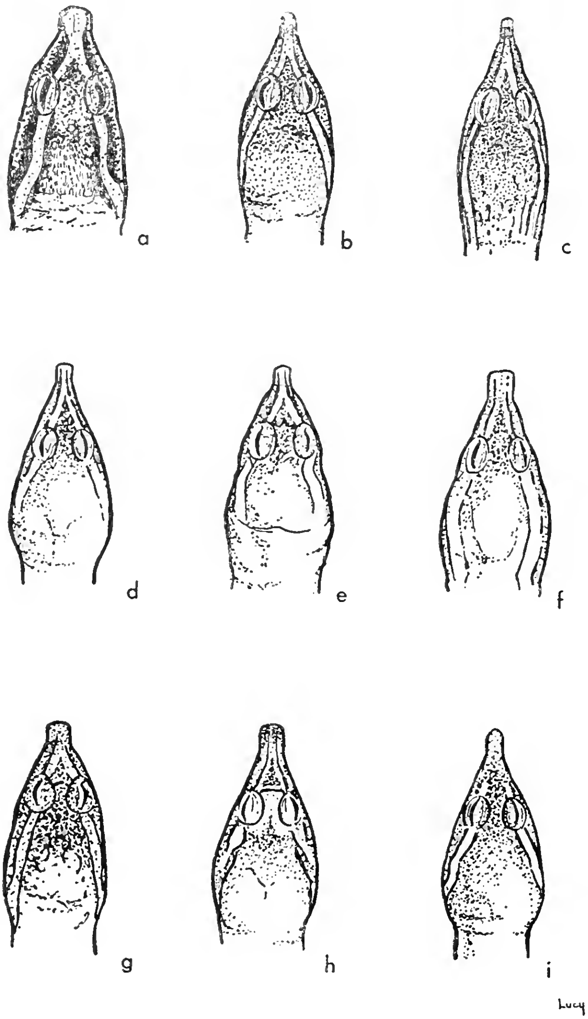

FIG. 5. Pattern on dorsal surface of snout of some American species and subspecies of the genus *Trionyx*. Note the gradual transition in pattern from that of *hartwegi* (b) and *asper* (c) to that of *emoryi* (h).

a. *T. ferox* (UMMZ 102276, × ⅓)
b. *T. spinifer hartwegi* (KU 46742, × ¾)
c. *T. spinifer asper* (KU 50842, × 1)
d. *T. spinifer pallidus* (KU 2958, × ½)
e. *T. spinifer pallidus* (KU 2934, × ½)
f. *T. spinifer pallidus* (KU 2947, × ½)
g. *T. spinifer guadalupensis* (TU 10165, × ⅔)
h. *T. spinifer emoryi* (KU 48218, × ⅔)
i. *T. muticus muticus* (KU 48236, × ⅔)

Geographic Variation

Geographic variation occurs in *Trionyx spinifer* and *T. muticus.* The variant populations of *spinifer* are segregated into six subspecies, those of *muticus* into two. In the subspecies of *spinifer* there is both group variation and clinal variation.

Group Variation

The six subspecies of *spinifer* can be separated into two groups on the basis of the juvenal pattern. One group (subspecies *spinifer, hartwegi* and *asper*) has a pattern of dark spots or ocelli of various sizes on the carapace, whereas the other group (subspecies *pallidus, guadalupensis* and *emoryi*) has a pattern of small white dots or tubercles on the carapace. The two groups differ also in the manner in which the mottled and blotched pattern first appears on the carapace of females. Usually, contrasting lichenlike figures initially surround the dark spots or ocelli on the carapace in females of the *spinifer* group (less evident in *pallidus*), whereas females of the *emoryi* group usually lack a contrasting pattern early in ontogeny. In general, the two groups differ in the degree of pigmentation. The *spinifer* group has larger marks and more contrasting patterns on the head and limbs, and more extensive pigmentation on the ventral surface than members of the *emoryi* group. *T. ater* is more closely related to those subspecies of the *emoryi* group but differs in having the ventral surface heavily speckled with black and an over-all blackish, dorsal coloration; the underlying pattern of *ater* resembles that of *emoryi.*

Clinal Variation

Several characters are arranged in a geographical gradient or cline. Some characters are relatively uniform and represent a terminus in the *spinifer* group. Some characters change gradually and successively through the subspecies *pallidus* and *guadalupensis,* and terminate in *emoryi* and *T. ater.* Some characacters of *ater,* in turn, show affinity with *T. muticus* and *T. ferox.*

Pattern on Snout

The pattern (Fig. 5) on the snout usually consists of pale, dark-bordered stripes that form an acute angle in front of the eyes in *spinifer, hartwegi* and *asper,* but the corresponding marks form a dark triangle the base line of which joins the anterior margins of the orbits in *emoryi* and usually in *guadalupensis.* In *pallidus,* the geographic range of which is between *guadalupensis* and *hartwegi,* there are different patterns that are in various degrees intermediate between those described immediately above for *hartwegi* and *guadalupensis.*

Pattern on Side of Head

The change in pattern (Fig. 6) and its contrast with the ground color on the side of the head parallels the sequence of changes in pattern on the snout. The pattern on the side of head contrasts with the ground color and consists of dark markings below the eye and on the neck, an indication of a postlabial stripe, and a pale, dark-bordered postocular stripe that may be variously interrupted (*spinifer* and *hartwegi; asper* usually has uninterrupted postocular and postlabial stripes that unite on the side of the head). The pattern is contrasting but variable in *pallidus. T. s. emoryi* and usually *guadalupensis* have fewer dark markings, sometimes none, and an interrupted postocular pale stripe that produces a pale blotch just behind the eye.

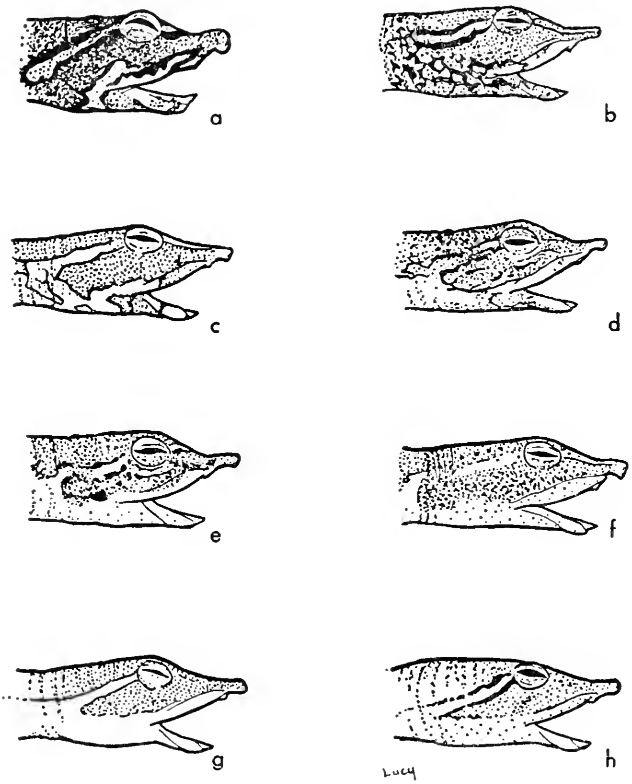

FIG. 6. Pattern on side of head of some American species and subspecies of the genus *Trionyx*. Note the gradual reduction in contrast of pattern and interruption of the postocular stripe from that of *spinifer* (b) to that of *emoryi* (f).

a. *T. ferox* (UMMZ 102276, × ⅓)
b. *T. spinifer spinifer* (UMMZ 54401, × ⅔)
c. *T. spinifer asper* (KU 50843, × ⅔)
d. *T. spinifer pallidus* (KU 50830, × ¾)
e. *T. spinifer guadalupensis* (SM 659, × ⅔)
f. *T. spinifer emoryi* (KU 2922, × ¾)
g. *T. muticus muticus* (KU 48228, × ⅔)
h. *T. muticus calvatus* (KU 47117, × ⅔)

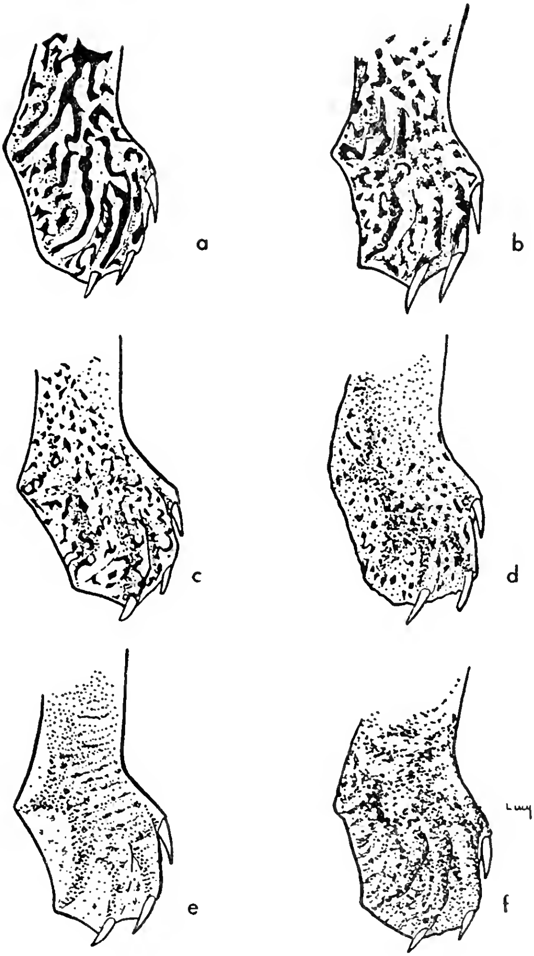

FIG. 7. Pattern on the dorsal surface of the distal part of the right hind limb of some American species and subspecies of the genus *Trionyx*. Note the gradual reduction in contrast of pattern from that of *hartwegi* (a) to that of *emoryi* (d).

a. *T. spinifer hartwegi* (KU 15932, × ¾)
b. *T. spinifer pallidus* (KU 40175, × ⅔)
c. *T. spinifer guadalupensis* (TU 10165, × ¾)
d. *T. spinifer emoryi* (KU 3153, × ⅚)
e. *T. muticus muticus* (KU 48228, × ¾)
f. *T. ferox* (UMMZ 102276, × ½)

FIG. 8. Shape of tubercles on anterior edge of carapace in some American species and subspecies of the genus *Trionyx* (× ½). Note the gradual reduction in size of tubercles from that of *hartwegi* (b) to that of *muticus* (h).

a. *T. ferox* (UMMZ 90010)
b. *T. spinifer hartwegi* (KU 3346)
c. *T. spinifer pallidus* (TU 13213)
d. *T. spinifer guadalupensis* (TU 10160)
e. *T. spinifer emoryi* (KU 2906)
f. *T. ater* (KU 46906)
g. *T. muticus muticus* (KU 48229)
h. *T. muticus muticus* (KU 48232)


a
b
c
d
e
f
g
h
Lucy

Pattern on Dorsal Surface of Limbs

A corresponding sequence of change occurs in the size of dark markings on the dorsal surface of the limbs (Fig. 7). The hind limb usually has larger markings than the forelimb. The change is gradual from larger and darker markings (contrasting pattern) in *hartwegi, spinifer* and *asper* to smaller and paler markings (non-contrasting pattern) in *emoryi.*

Tuberculation

There is also a cline in tuberculation (Fig. 8) that parallels geographically the sequence of changes in patterns mentioned immediately above. The size of the tubercles along the anterior edge of the carapace changes in both sexes from those that are enlarged and equilateral or conical in shape in *spinifer, hartwegi, asper* and *pallidus* to those that are scarcely elevated in *guadalupensis, emoryi* and *T. ater.* Indeed, in the three kinds mentioned last, the tubercles are absent in some specimens. There seems to be a corresponding reduction in the size and number of small, sharp-tipped tubercles that cover the carapace in adult males; the carapace of *T. ater* is mostly smooth and has only a few small, whitish tubercles.

Ratios

The clinal tendencies in PL/HW (Fig. 3) and CL/CW (Fig. 4) that parallel those mentioned above for pattern and tuberculation have already been mentioned under the section "Ontogenetic Variation."

The ratio of CL/PCW (Fig. 9) was used in an effort to show further differences in the shape of the carapace, especially the plane on the carapace

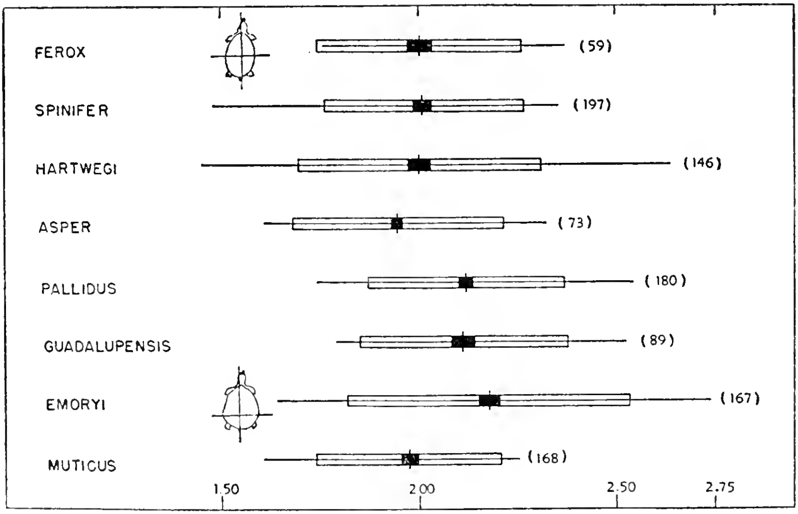

FIG. 9. Anteroposterior position of plane of greatest width of carapace (CL/PCW) in some American species and subspecies of the genus *Trionyx.* Symbols as in Fig. 3. The greatest width of carapace is midway between anterior and posterior ends in *ferox, spinifer, hartwegi, asper* and *muticus,* and farther posterior in the other subspecies of *spinifer.*

where the greatest width occurs. Figure 9 shows the greatest width to be approximately midway between the anterior and posterior ends in the subspecies *spinifer, hartwegi* and *asper,* and in the species *ferox* and *muticus* (CL/PCW of 2.00). The greatest width of carapace is more posterior and at approximately the same plane in *pallidus* and *guadalupensis,* and farther posterior in *emoryi.* Calculated ratios for 12 specimens of *T. ater* average 2.15, a value that suggests closer affinity with *pallidus, guadalupensis* and *emoryi* than to the other species and subspecies.

Comparison of the relative lengths of snout (HW/SL, Fig. 10) in different populations of *T. spinifer* shows a character gradient. To facilitate a comparison utilizing large samples, the subspecies *spinifer* was combined with *hartwegi,* and *pallidus* with *guadalupensis.* The snout is longer in the subspecies *spinifer* and *hartwegi* than in *emoryi;* the length of the snout of *emoryi* resembles that of *T. ferox.* The snout is proportionately the longest in *T. muticus.* The average ratio of HW/SL for 12 individuals of *T. ater* is 1.37, and is nearer that of *pallidus, guadalupensis, emoryi* and *ferox* than that of *muticus* or the other subspecies of *T. spinifer.*

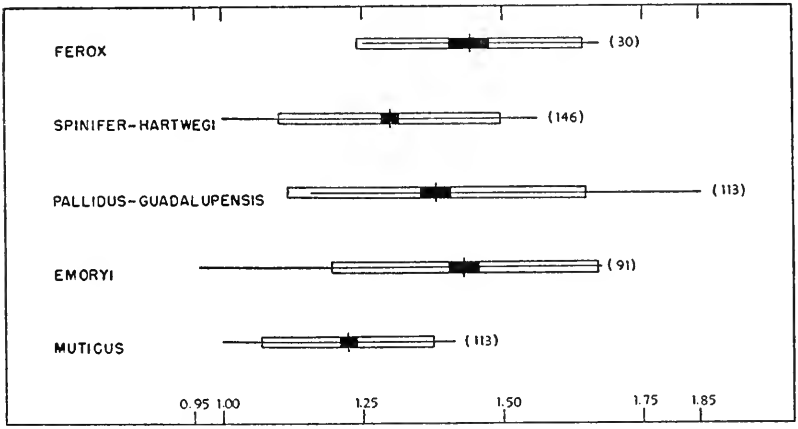

FIG. 10. Ratio of width of head to length of snout (HW/SL) in some American species and subspecies of the genus *Trionyx.* Symbols as in Fig. 3. Values for *spinifer* are combined with those of *hartwegi,* and those of *pallidus* with *guadalupensis.* The snout is proportionately the longest in *muticus.*

Size of the ocelli increases from west to east in populations of *T. spinifer* in the upper Mississippi River and Great Lakes drainages.

The ratio of OD/PL (Fig. 11) varies considerably but gradually increases from Kansas northeastward to Michigan. The minimal diameter of any ocellus recorded was one millimeter; solid dots on the carapace (*hartwegi*) were also recorded as one millimeter. Larger ratios are usually derived from measurements of larger individuals. Seemingly, there should be a clinal tendency in ontogenetic variation paralleling the size of ocelli and dependent on it; ontogenetic variation should be least in western populations in which the size of ocelli does not change appreciably with increasing size, and should be greatest in eastern populations in which the ocelli on adult males are larger than those on the carapace of young turtles. It is difficult to demonstrate

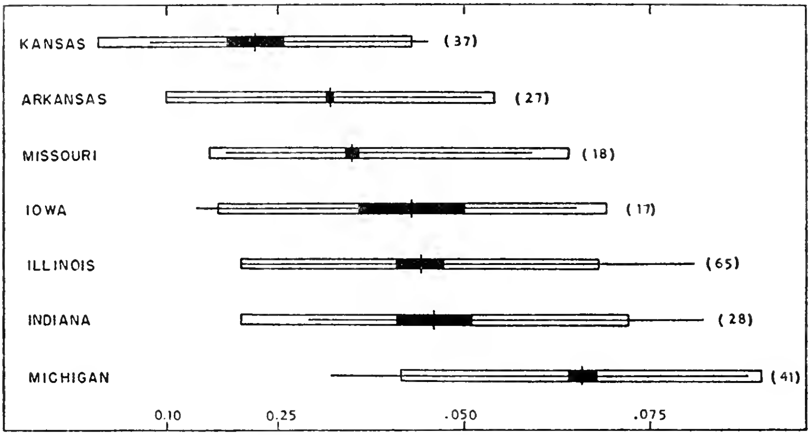

FIG. 11. Ratio of diameter of ocellus to length of plastron (OD/PL) in *T. spinifer* from some states in the upper Mississippi River and Great Lakes drainages. Symbols as in Fig. 3. The size of the ocelli on the carapace gradually increases from Kansas northeastward to Michigan.

ontogenetic variation because specimens of corresponding size from the same general area may have ocelli of different sizes. The gradient in size of ocelli is also indicated by specimens from other states. I have the subjective impression that there is least variation in specimens from Michigan (Great Lakes-St. Lawrence River drainage), but this is not clearly shown by Figure 11.

Character Analysis

Snout

The snout (Fig. 12) is tubate having terminal nostrils separated by a vertical septum. One of the principal characters distinguishing *T. ferox* and *T. spinifer* from *T. muticus* is a lateral, whitish ridge projecting from each side of the nasal septum (hereafter referred to as septal ridges but often referred to in the literature as a papilla). The shape of the end of the snout is truncate in *T. ferox* and *T. spinifer,* and the nostrils are larger than in *T. muticus.* In *muticus* the snout usually terminates somewhat obliquely, and the nostrils tend to be slightly inferior; also, the end of the snout is usually rounded and somewhat pointed, causing the nostrils to be visible in lateral view. Some *T. muticus* do not differ markedly from *ferox* or *spinifer* in shape of the end of the snout. Stejneger (1944:14) mentioned indication of a septal ridge that did not reach the opening of the nostril in *muticus.* I have slit the outer edge of the nostril on several specimens of *muticus,* and have not noticed an indication of a septal ridge.

Tuberculation

Tubercles or obtuse prominences occur on the anterior edge of the carapace (Fig. 8) or on the dorsal surface of the carapace. *Trionyx muticus* lacks tubercles, although some individuals show shallow, widely spaced wrinkles that suggest prominences on the anterior edge of the carapace. Both sexes of *T. ferox* have prominences, resembling flattened hemispheres, on the anterior edge of the

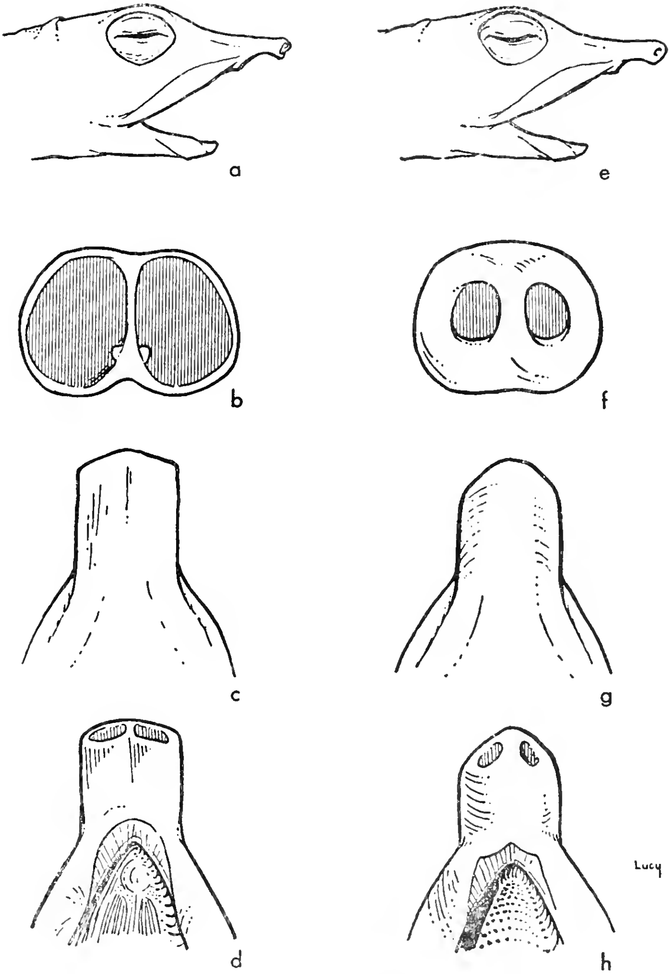

FIG. 12. Shape of snout in *T. spinifer* (left, a-d, from KU 46907) and *T. muticus* (right, e-h, from KU 48236). Lateral views—a, e (× 1); anterior views—b, f (× 5); dorsal views—c, g (× 2.5); ventral views—d, h (× 2.5).

carapace and in the nuchal region. Large females of *ferox* have obtuse prominences in the center of the carapace posteriorly, some of which are often arranged in longitudinal rows. The surface of the carapace in both sexes of *T. ferox* has small closely-set, blunt tubercles arranged in rows that resemble longitudinal ridges (most evident in juveniles).

Large females of *T. spinifer* have obtuse prominences in the center of the carapace posteriorly, some of which in many specimens are arranged in longitudinal rows; I cannot discern any correlation of number or arrangement of prominences with size in *spinifer* or *ferox*. The carapace in adult males of *spinifer* bears small, sharp tubercles that make the surface feel like sandpaper. The tubercles on the anterior edge of the carapace in adults of both sexes vary from round to equilateral and conical to low and flattened (see comments on tuberculation under subsection entitled "Geographic Variation"). Some large females of the same subspecies have tubercles on the anterior edge of the carapace that may be conical (higher than wide) or equilateral. The difference in shape of the tubercles seems not to be correlated with size because one *T. s. pallidus,* 30.5 centimeters (TU 13212) has prominent but blunted and equilateral tubercles, whereas, another female of *pallidus,* 20.8 centimeters (TU 13210), from the same locality has higher, conical tubercles. The blunted, equilateral tubercles may be the result of environmental wear, or the difference in shape of tubercles may be due to individual variation.

Pattern on Carapace

Two features of the pattern on the carapace are of taxonomic worth: 1) the width and distinctness of the pale rim at the periphery of the carapace (marginal rim), if present, and 2) the kind of pattern on the carapace (juvenal pattern). The marginal rim is absent in females of *T. ater,* and only faintly evident in males. The marginal rim is obscured or absent (adult males and females) and is not separated from the ground color of the carapace by a dark marginal line in hatchlings of *T. ferox*. The carapace of *T. muticus* has a marginal rim that is usually separated from the ground color of the carapace by an ill-defined, dark marginal line; some individuals lack the marginal dark line. The subspecies of *T. spinifer* have a well-defined, dark, marginal line that separates the marginal rim from the ground color of the carapace; *T. s. asper* has more than one dark marginal line on the carapace. The marginal rim is ill-defined and blotched, or absent, in large females of all species of *Trionyx*.

The marginal rim is widest at the posterior end of the carapace and lacking in the nuchal area. The width of the pale marginal rim is very narrow, almost to the degree of being absent, in juveniles of *T. ferox*. *T. s. emoryi* has a pale, marginal rim that is four or five times wider posteriorly than it is laterally, whereas posteriorly the width of the rim in the other subspecies of *T. spinifer* and in the species *T. muticus* is only two or three times wider posteriorly than it is laterally.

The juvenal pattern commonly consists of whitish tubercles or dots (*T. s. emoryi, T. s. guadalupensis, T. s. pallidus, T. ater*), large black ocelli (*T. s. spinifer*), small black dots and ocelli (*T. s. hartwegi, T. s. asper*), large dusky spots or ocelli (*T. m. calvatus*), or small dusky dots or short streaks and dashes (*T. m. muticus*). Some hatchlings of *pallidus* and *emoryi* have a uniform pale brown or tan carapace; hatchlings of *T. ferox* have a distinctive pattern (Pl. 31).

Further comments and illustrations pertaining to kind of pattern on the carapace are offered under the accounts of species and subspecies.

Pattern on Dorsal Surface of Snout (Fig. 5)

T. ferox has pale stripes on a dark background that unite in front of the eyes; the dark ground color becomes paler with increasing size, but the stripes retain thick black borders. *T. m. muticus* has ill-defined, pale stripes that are evident just in front of the eyes and do not extend anteriorly to unite in front of the eyes, whereas *T. m. calvatus* lacks pale stripes on the snout. The kind of pattern on the dorsal surface of the snout that is characteristic for each of the subspecies of *T. spinifer* has been mentioned in the discussion of clinal variation.

Pattern on Side of Head (Fig. 6)

T. ferox has a pale broad, postocular stripe in contact with the orbit or not, and other pale marks on a dark background; the ground color becomes paler with increasing size, but the stripes and other marks retain thick black borders. *T. m. muticus* usually has an uninterrupted, dusky-bordered, postocular stripe, whereas *T. m. calvatus* (in adult males only) has pale postocular stripes with thick blackish borders. The pattern on the side of head that is characteristic for each subspecies of *T. spinifer* has been mentioned in the discussion of clinal variation.

Pattern on Dorsal Surface of Limbs (Fig. 7)

Young specimens of *T. ferox* have pale marks on a blackish background. As growth proceeds the distinctive contrasting pattern is obliterated and eventually is replaced by a uniform grayish coloration in large adults. The pattern on the limbs of *T. muticus* is not contrasting, and is almost a uniform grayish, consisting of fine, pale markings. The clinal variation in pattern and kind of pattern on the limbs of the subspecies of *T. spinifer* has been mentioned in the discussion of clinal variation. Dark markings tend to form streaks that are coincident with the digits, and larger markings occur on the hind limbs than on the forelimbs.

Marginal Ridge

The anterolateral edge of the carapace in *T. ferox* (both sexes and all sizes) is "folded over" into a ridge having a distinct inner margin (Pls. 1 and 2), which is hereafter referred to as the marginal ridge. Siebenrock (1924:184-85) referred to this ridge as a "Hautsäume" and mentioned its occurrence in Old World species of the genus *Trionyx*. The marginal ridge is not present in *T. muticus, T. spinifer* or *T. ater.*

Ratios

The means of some samples (Fig. 3) differ in regard to PL/HW, but the ranges of variation overlap so much that little significance can be attributed to the difference. *T. ferox*, and to a lesser extent *T. s. emoryi* and *T. s. asper,* have slightly larger heads than the other forms. The width of head is proportionately the smallest in *T. muticus;* in most individuals of it having a plastron so long as 13.0 centimeters, the width of the head is less than 16 per cent of the length of the plastron—a percentage that is distinctive.

The visibly narrower carapace (CL/CW, Fig. 4), suggesting an ovoid or oblong shape, in some large individuals of *T. ferox* and *T. s. emoryi* is indicated by the large ratio in specimens that have a plastral length of 8.0 centimeters or more. Nevertheless, the degree of overlap of the ranges of variation is such that this ratio is of relatively little use taxonomically.

The greatest width of the carapace is farther posterior in *T. s. emoryi* than in the other forms (CL/PCW, Fig. 9). The considerable overlap of the range of variation of this ratio for *emoryi* with the other forms limits its usefulness as a taxonomic character.

The snout is proportionately shortest in *ferox* and *T. s. emoryi,* and longest in *muticus* (HW/SL, Fig. 10). The most marked difference in this ratio is between the species *muticus* and *ferox;* the ranges of variation of those species overlap to a degree that tends to negate the taxonomic usefulness of this character.

Most adults and subadults of *T. ferox* show clearly in dorsal view the anterolateral portions of the plastron. This condition is much less well developed in some specimens of *T. s. emoryi.* *T. ferox* is extreme in the ratio CL/PL (relatively the longest plastron or shortest carapace, Fig. 13). *T. s. asper* has the shortest plastron in relation to length of carapace. Calculated ratios for 12 *T. ater* average 1.36, a value that suggests close affinity with some subspecies of *T. spinifer* (*pallidus, guadalupensis, emoryi*). Because of the degree of overlap of the ranges of variation in all forms, little significance can be attributed to the difference in means of *ferox* and *asper.*

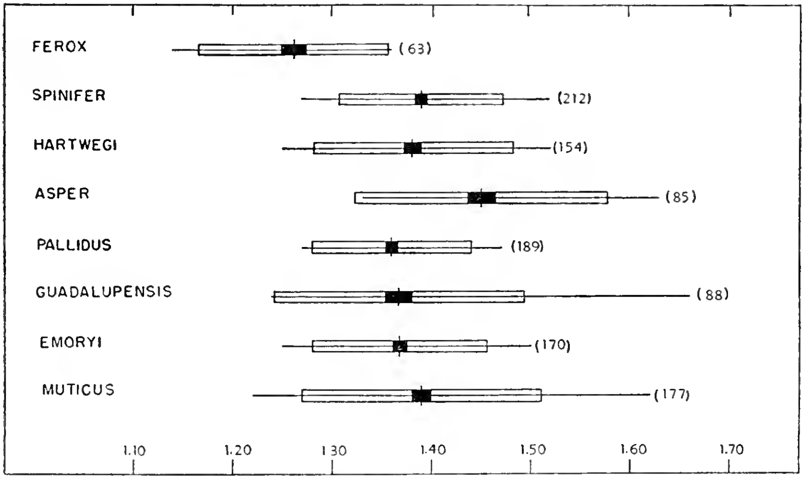

FIG. 13. Ratio of length of carapace to length of plastron (CL/PL) in some American species and subspecies of the genus *Trionyx*. Symbols as in Fig. 3. *T. ferox* has proportionately the shortest carapace.

Scalation

Cornified, smooth or cusplike areas occur on each limb, but their number and arrangement are of no taxonomic value. Normally, the anterior surface of each forelimb possesses four cornified areas for which the term antebrachial scales is proposed (Fig. 14). Two of the four scales occur in a more dorsal position; the lateral edge of the proximal one is free and cusplike along a part of its length, whereas the distal scale is smooth-edged. Two scales having their lateral edges free and cusplike are ventral in position, and closer together than the two dorsad scales. Size of the scales and length of the free cusplike edges vary. Occasionally adjacent scales are fused or small additional scales are present. The number, configuration and arrangement of the two cornified areas on each hind limb are constant. One of these scales is smooth-edged and occurs posteriorly on the dorsal surface. The other scale, situated on the ventral surface posteriorly in the region of the heel and distal to the smooth-edged scale of the dorsal surface, has a pronounced, cusplike, free edge.

FIG. 14. Dorsal surface of right forelimb showing normal number and arrangement of antebrachial scales in American species of the genus *Trionyx* (*T. spinifer hartwegi*, KU 15932, × ¾).

Choanal Papillae

This term refers to the papillate flaps of skin that project from the lateral borders of the internal nares. Webb and Legler (1960:23) noted their presence in softshells, and Parsons (1958) discussed their occurrence in sea turtles of the family Cheloniidae and in the testudinid subfamily Emydinae (1960). In preserved softshells the choanal papillae may extend laterally and partly cover the nares, or may be folded vertically against the lateral borders of the nares; in the latter position the papillae are easily overlooked. To my knowledge, choanal papillae occur in all American species and subspecies of soft-shelled turtles. The free edge of each narial flap shows various degrees of fimbriation. The fimbriated border is least developed (margin nearly entire) in *T. muticus* and most developed in *T. ater* and *T. ferox*. In *ater* at least, the anteriormost portions of the narial flaps seem wider than in the other forms and show a greater degree of fimbriation than the posteriormost parts. The choanal papillae are most easily observed in large specimens.

Skull

In general, there is less difference between the skulls of *ferox* and *spinifer* than between either of those species and *muticus* (Stejneger, 1944:10-11). Figure 15 shows the general differences in proportions of the skulls of *spinifer* and *muticus;* Plate 54 shows the skull of the holotype of *Platypeltis agassizi* (= *T. s. asper*), which is similar to that of *ferox;* Stejneger (*op. cit.*) provided labelled drawings of the skull of *T. spinifer* as well as photographs of skulls of other forms.

The total of 159 skulls examined by me include 80 of *spinifer*, 50 of *ferox*, and 29 of *muticus*. There are no secondary sexual differences between skulls of corresponding size, except in *agassizi*-form skulls mentioned under the account of *T. s. asper*, and possibly in *ferox*. Most, and possibly all, of the skulls of *muticus* having a basicranial length of 40.0 millimeters or more, and those of *spinifer* exceeding 50.0 millimeters must represent females (by correlation of known maximum size of males with greatest width of head, which is, in turn, compared with the greatest width of skull and corresponding basicranial length).

Measurements used include basicranial length (occipital condyle to tip of upper jaw), greatest width (variable in position), greatest width of alveolar

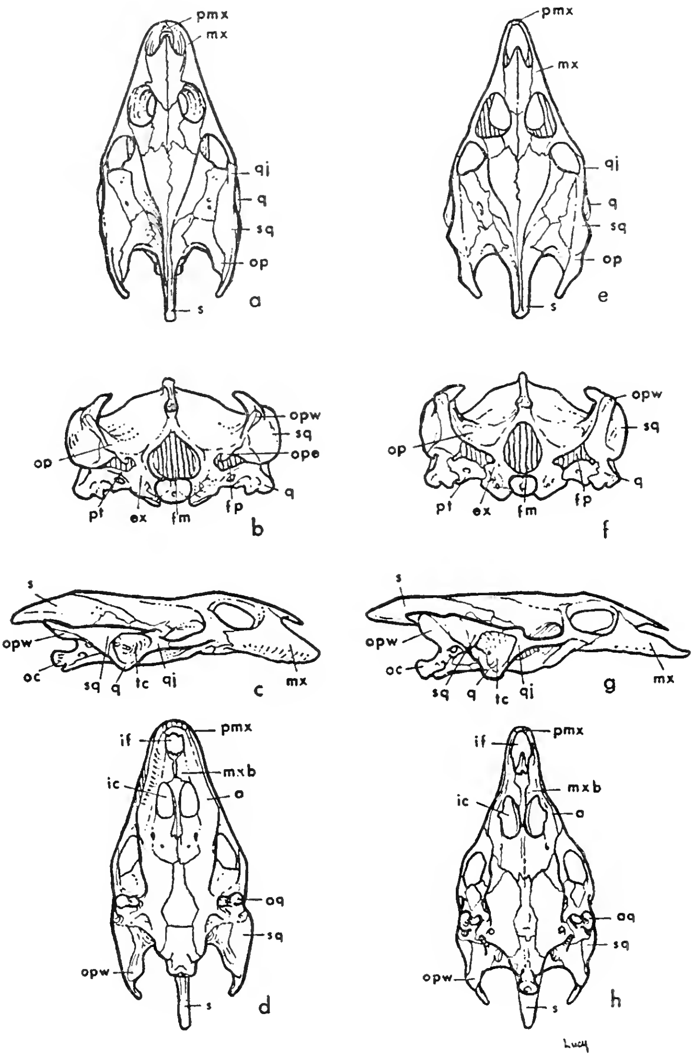

FIG. 15. Skulls of *Trionyx spinifer hartwegi* (left, a-d, KU 2757), and *Trionyx muticus muticus* (right, e-h, KU 1870). Dorsal views, a (× ½), e (× ¾); occipital views, b (× ⅚), f (× 1); lateral views, c (× ½), g (× ¾); ventral views, d (× ½), h (× ¾).

a., alveolar surface of upper jaw
aq., articular surface of quadrate
ex., exoccipital
fp., fenestra postotica
fm., foramen magnum
if., intermaxillary foramen
ic., internal choana
mx., maxilla
mxb., maxillary bridge
oc., occipital condyle
op., opisthotic
ope., opisthotic-exoccipital spur
opw., opisthotic wing
pmx., premaxillaries (fused)
pt., pterygoid
q., quadrate
qj., quadratojugal
sq., squamosal
s., supraoccipital spine
tc., tympanic cavity

surface of maxilla (taken at level immediately posterior to anterior margin of internal choanae), greatest length of internal choanae, and least breadth of maxillary bridge (separating internal choanae and intermaxillary foramen). One ratio developed from the measurements was greatest length of internal choanae/least breadth of maxillary bridge, hereafter referred to as IC/MB. This ratio is discussed under the account of *T. s. asper.*

Greatest Width

The position or level on the skull where the greatest width (Table 3) occurs is of some diagnostic value in distinguishing the skulls of *ferox* from *spinifer* and *muticus.* Skulls of *ferox* usually are widest at the level of the quadratojugal (immediately in front of tympanic cavity), whereas skulls of *spinifer* and *muticus* usually are widest slightly more posteriorly at a level on the squamosal immediately behind the tympanic cavity. Occasionally the width at the level of the quadratojugal and squamosal is the same, or the greatest width of skull may be ventrad between the quadrates, which are slightly flared laterally. The latter condition possibly is most prevalent in *muticus.*

TABLE 3. VARIATION IN POSITION OF GREATEST WIDTH OF SKULL OF NORTH AMERICAN SPECIES OF THE GENUS TRIONYX (EXCLUDING ATER). THE NUMBER OF SPECIMENS EXAMINED (IN PARENTHESES) FOLLOW THE SPECIFIC NAMES.

POSITION	Species		
	ferox (36)	*spinifer* (47)	*muticus* (14)
Squamosal	7 (19%)	35 (74%)	11 (79%)
Quadratojugal	26 (72%)	7 (15%)	1 (7%)
Quadrate	2 (6%)	....	2 (14%)
Squamosal and quadratojugal of same width	1 (3%)	5 (11%)	....

Supraoccipital Spine

The ventral surface of the supraoccipital spine in *muticus* lacks a medial ridge, and gradually increases in width anteriorly, so that it is widest proximally in the region of the roof of the foramen magnum. In *ferox* and *spinifer,* the ventral surface, usually having a medial ridge, is narrow and of the same width throughout its length or somewhat flared distally. The ventral surface of the supraoccipital spine, which is widest proximally in *muticus,* is always narrow proximally in *ferox* and *spinifer.* The ventral surface of the supraoccipital spine of one skull of *spinifer,* USNM 91311, differs little from that of *muticus.*

Foramen Magnum

The shape of the foramen magnum is generally rhomboidal in *spinifer* and *ferox;* the ventral angle is semicircular, the lateral angles obtuse, and the dorsal angle more acute. The shape of the foramen magnum in *muticus* is ovoid, higher than wide; the sides are evenly rounded.

Opisthotic-Exoccipital Spur

Skulls of *spinifer* normally have the fenestra postotica partly restricted by a medially-slanting, descending spur from the roof of the fenestra postotica; the spur incorporates the suture between the exoccipital and opisthotic and includes parts of those two bones. On one skull (KU 2824) the spur is displaced more medially and does not incorporate the opisthotic. The descending spur contacts the pterygoid ventrally forming a complete bony strut traversing the fenestra postotica in some skulls (KU 2228, 2666, 2762, TU 15423, MCZ 46621, TU 15415, right side only). The fenestra postotica on skulls of *ferox* and especially *muticus* is not normally restricted by an opisthotic-exoccipital spur.

Often the spur is reduced and indicated by a smooth projecting ridge. Sometimes the spur or ridge is absent on skulls of *spinifer*, and I have seen no well-developed spur on a skull of *muticus*. The development of the spur is not due to ontogenetic variation. There is some variation in development of the spur on either side of the skull; two skulls of *ferox* have the combination ridge/absent, and two of *spinifer* have the combinations ridge/spur and spur/absent. The frequency (based on counts of individual skulls) and the degree of development of the spur among the three species in indicated in Table 4.

TABLE 4. FREQUENCY AND DEGREE OF DEVELOPMENT OF OPISTHOTIC EXOCCIPITAL SPUR OF NORTH AMERICAN SPECIES OF THE GENUS TRIONYX (EXCLUDING ATER). THE NUMBER OF SPECIMENS EXAMINED (IN PARENTHESES) FOLLOW THE SPECIFIC NAMES.

DEVELOPMENT OF SPUR	Species		
	ferox (43)	*spinifer* (68)	*muticus* (29)
spur (well-developed)	1 (2%)	45 (66%)	....
ridge (reduced)	7 (16%)	20 (30%)	1 (3%)
absent	35 (82%)	3 (4%)	28 (97%)

Loveridge and Williams (1957:415, footnote) cited Siebenrock who mentioned a descending process of the opisthotic in *Dogania* (= *Trionyx*) *subplana* and *Trionyx sinensis.* I have not seen an ascending process of the pterygoids on skulls of American softshells as described by Loveridge and Williams (*op. cit.*:414, 429, fig. 54) for *Lissemys, Cyclanorbis, Cycloderma* and some *Trionyx triunguis.*

Opisthotic Wing

This term refers to the laterally directed, posterior part of the opisthotic that is visible in occipital, lateral and ventral views. In ventral view the opisthotic wing is most easily seen and is wider in *muticus* than in *spinifer* or *ferox.* In *muticus* the distal part is truncate, whereas in *ferox* and *spinifer*, it is more tapered and gently rounded, although somewhat unevenly flared medially. Also there is more of a downward curvature (in ventral view) of the opisthotic wing in *muticus* than in *ferox* or *spinifer*; consequently the tip of the wing in *muticus* is often just visible in dorsal view (on lateral side of squamosal), certainly in lateral view. The distal part or tip of the opisthotic wing is not visible in dorsal view on skulls of *ferox* or *spinifer*.

Articular Surface of Quadrate

The ventral surface of the quadrate that articulates with the mandible is composed of a lateral condyle and a medial articular surface. The condyle and medial articular surface are separated by a furrow. On skulls of *ferox* and *spinifer* the lateral condyle, which is not conspicuously tapered posteriorly, is slightly larger than the medial articular surface, and the furrow is shallow. On skulls of *muticus*, the lateral condyle is conspicuously tapered posteriorly, is slightly smaller than the medial articular surface, and the furrow is deep.

Contact of Maxillaries Above Premaxillaries

The contact of the maxillaries above the premaxillaries is of diagnostic value in distinguishing skulls of *ferox* and *spinifer* from those of *muticus*. I have seen no skulls of *muticus* on which the maxillaries were in contact, and no skulls of *ferox* on which the maxillaries were separated. Stejneger (1944:19), however, reported a skull of *muticus* (USNM 102677) having the maxillaries in contact. Maxillaries are in contact (sometimes just barely) in 65 of 74 skulls of *spinifer* (88%); the premaxillaries are separated on nine skulls (12%).

Carapace

The dorsal surface of the bony carapace of American trionychids consists of a nuchal, seven or eight pairs of pleurals, and seven or eight, rarely nine, neurals (Fig. 16). The lateral parts of the nuchal overlie the second pair of ribs. The distal parts of the second through the ninth pair of ribs extend laterally beyond the lateral edges of the pleurals. There are no marginal ossifications. The posterior part of the bony carapace bears blunt, rounded or ovoid to linear, prominences mostly on the last pair of pleurals principally on large females of *spinifer* and *ferox;* I have seen only one adult male (stuffed, MCZ 46633) having a semblance of welts on the bony carapace. The nuchal, pleurals and neurals are sculptured.

As growth proceeds, the single, transversely-oriented, fontanelle of young turtles that separates the nuchal from the first neural and first pair of pleurals divides into two fontanelles that generally decrease in size and finally disappear. Occasionally only one (unilateral) large fontanelle is present (USNM 54734, *muticus*). The largest specimens noted that retain fontanelles are a *ferox* (USNM 029474) having a plastron 24 centimeters long, and a *spinifer* (USNM 54731) having a plastron 20 centimeters long. The fontanelles probably are present in some larger individuals.

Most variation concerns the number of neurals and pairs of pleurals, and their arrangement posteriorly (H. M. Smith, 1947:121, table; Stejneger, 1944:18). Table 5 shows the frequency of occurrence of the number of neurals, pairs of pleurals, and the separation or contact of the seventh pair of pleurals; figure 16 illustrates some of the configurations of these plates posteriorly (e, g, and i not

FIG. 16. Carapace of *Trionyx spinifer* (a), and sketches of posterior parts of carapaces (b-i) of three American species, showing number and variation in arrangement of neurals and pleurals (not to scale; seventh neural, n7, and pleural, p7).

a. KU 2226, Lewisville, Lafayette County, Arkansas (× ⅓); sculpturing incompletely shown. Labels: r, ribs; nu, nuchal; n, neurals 1-7; p, pleurals 1-7.
b. *ferox*, USNM 60496, Auburndale, Polk County, Florida.
c. *muticus*, KU 1964, Doniphan Lake, Doniphan County, Kansas.
d. *spinifer*, USNM 100380, Plaquemine, Iberville Parish, Louisiana.
e. *muticus*, TCWC 7260, Red River, 8 mi. NW Ringgold, Montague County, in Clay County, Texas.
f. *spinifer*, USNM 59266, Homer, Winona, Minnesota.
g. *muticus*, KU 2840, White River, DeVall's Bluff, Prairie County, Arkansas.
h. *muticus*, USNM 115939, Mississippi.
i. *muticus*, USNM 54734, Mississippi River, Fairport, Muscatine County, Iowa.

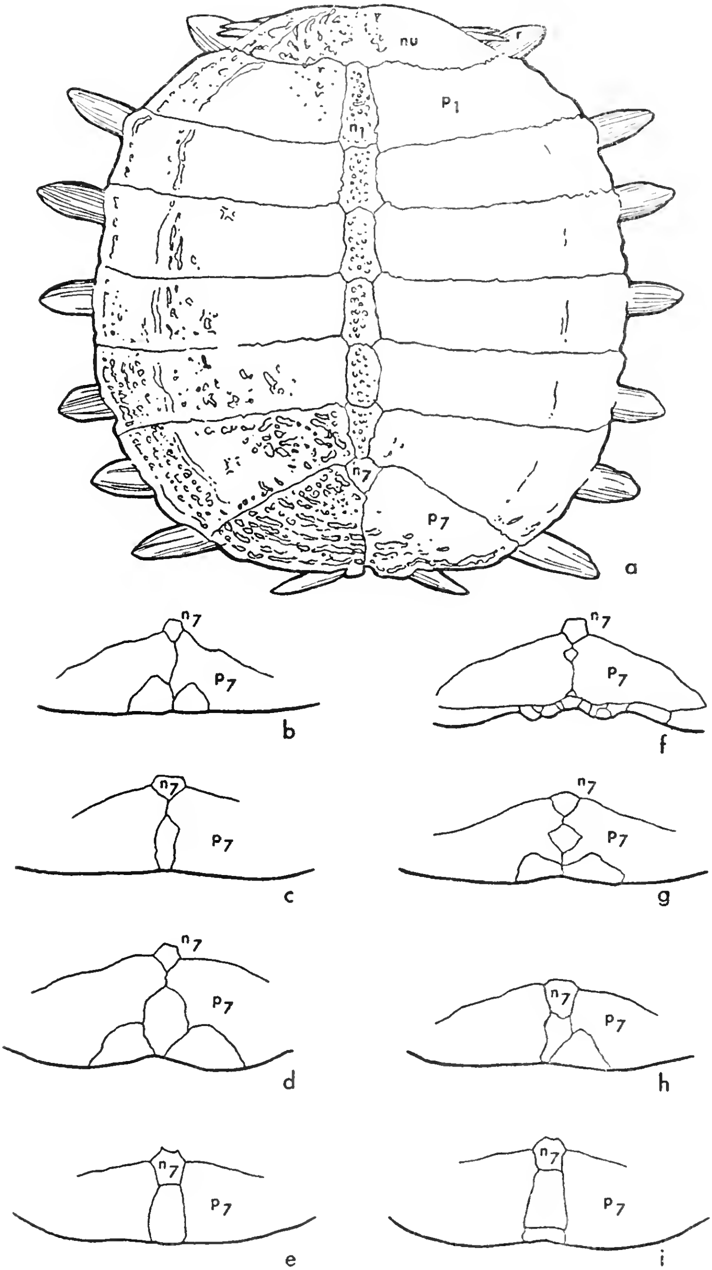
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TABLE 5. FREQUENCY OF OCCURRENCE OF NUMBER OF NEURALS, PAIRS OF PLEURALS, AND SEPARATION OR CONTACT OF THE SEVENTH PAIR OF PLEURALS AMONG SPECIES OF AMERICAN SOFT-SHELL TURTLES

Number		Contact (+) or separation (—) of seventh pair of pleurals	Species		
Neurals	Pairs of pleurals		*ferox* (16)	*spinifer* (60)	*muticus* (34)
7	7	+	9 (56%)	50 (83%)	13 (38%)
7	8	+	5 (31%)	2 (3%)	2 (6%)
8	7	+	2 (13%)	3 (5%)	3 (9%)
8	8	+	....	4 (7%)	2 (6%)
8	7	—	....	1 (2%)	14 (41%)

included in Table 5). The eighth pair of pleurals is reduced or absent (Loveridge and Williams, 1957:417). Eight neurals and eight pairs of pleurals occur in all three species. The seventh pleurals may contact each other in all three species, and their separation has been observed only in the species *spinifer* and *muticus*. Seven neurals and contact of the seventh pair of pleurals, or eight neurals and separation of the seventh pair of pleurals from each other occurs with approximately equal frequency in the species *muticus*. *T. ferox* and *spinifer* most often have seven neurals, seven pairs of pleurals, and the seventh pair of pleurals in contact. Stejneger (*loc. cit.*) mentioned a specimen in MCZ having nine neurals; I recorded nine neurals for USNM 54734 (Fig. 16i) for which Stejneger (*loc. cit.*) recorded eight. AMNH 57384 (*ferox*) has a small eighth pleural on the left side only, and USNM 115939 (*muticus*) has an eighth pleural only on the right side (Fig. 16h). Anomalous conditions observed included: an accessory bone between the first and second pleurals on the right side that contacts the first and second neurals in USNM 54733, (*muticus*); only six neurals in USNM 95193 (*spinifer*); a small accessory bony element between the first and second neurals in AMNH 57383 (*ferox*); and, only six pleurals (second and third fused) on the right side in USNM 54734 (*muticus*).

Ventrally, the bony carapace shows ten thoracic vertebrae, the second through the ninth having well-developed, depressed ribs that are fused (no sutures) to the pleurals. The ribs of the first thoracic vertebra are represented by bony struts that extend posterolaterally and contact the anterior borders of the second pair of ribs. The two ribs of the ninth pair are free for most of their length and often are broken; they are slightly shorter than the eighth pair of ribs. The ribs of the tenth thoracic vertebra may be well-developed (KU 2219, 2666, 50856, *spinifer*, and 16528, *ferox*), but are usually broken off and represented only by transverse processes.

Kyphosis

Kyphosis (angular curvature of the vertebral column) or the hump-backed condition in American softshell turtles has been summarized by Nixon and Smith (1949:28). Cahn (1937:185, pl. 25e) illustrated the condition in an individual of *T. spinifer*, and H. M. Smith (1947:119) mentioned kyphotic softshells representing the species *spinifer* (subspecies *hartwegi* and *emoryi*) and *muticus*. Neill (1951:10) mentioned two kyphotic *T. s. asper* and Nixon and Smith (*loc. cit.*) recorded the report of a kyphotic *T. ferox*. I have noted the condition in four *muticus* (subspecies *muticus*, KU 1959-60, 23230; INHS 2148) and seven *spinifer* (CNHM 22925; subspecies *hartwegi*, USNM 55689; subspecies *spinifer*, UMMZ 52948, 95615; subspecies *emoryi*, KU 2219, 33523, TU 16240). The smallest kyphotic specimen, a hatchling, TU 16240, has a plastral length of 3.5 centimeters. Kyphosis is to be expected in all kinds of softshells as are other abnormalities, such as albinism (reported for *Lissemys* by D'Abreu, 1928, and partial albinism noted in *T. cartilagineus* by Mohr, 1929) or congenital absence of limbs (reported by Dutta, 1931, as occurring in the genera *Trionyx* and *Lissemys*). The cause of kyphosis is not known. Smith (*op. cit.*:120) suggested an abnormally early fusion of the costals (= pleurals) with the ribs, and a subsequent differential rate of growth between them and the vertebral column as a hypothesis; Williams (1957:236) proposed that late retraction of the yolk mass, or retraction of an excessively large yolk mass may cause kyphosis. The cause of kyphosis may be of genetic origin or due to some environmental damage to the vertebral column prior to the cessation of growth. The variation in rate of growth of the vertebral column may produce humps of different shapes and sizes. Some of the specimens noted above (UMMZ 52948, 95615) have the carapace only slightly arched and are considered partly kyphotic. There seem to be degrees of kyphosis, a fact that should be taken into account in considering the occurrence of variation in greatest depth of shell.

Plastron

The plastron is united to the carapace by ligamentous tissue and is somewhat flexible anteriorly and posteriorly. Anteriorly the plastron is somewhat hingelike and may contact the anteriormost edge of the carapace. The bony elements are reduced. There is usually a median vacuity, which is relatively smaller in larger specimens and may be divided into two vacuities (a posteromedial and an anteromedial) by the medial juxtaposition of the hyo-hypoplastra, especially in *muticus*. Williams and McDowell (1952) have recommended a change in nomenclature for some of the plastral bones on the basis of reinterpretation of their homologies. The nine plastral bones include: an anterior pair of preplastra (= epiplastra, *auct.*); an unpaired, median bone, representing fused epiplastra (= entoplastron, *auct.*), hereafter referred to as the epiplastron; a pair of hyoplastra; a pair of hypoplastra; and, posteriorly, a pair of xiphiplastra (Fig. 17).

Siebenrock's (1902) synopsis of living trionychids was based entirely on plastral characters. He distinguished between *muticus* and *spinifer* principally by the shape of the epiplastron; *T. ferox* was not considered different from *spinifer*. The median angle formed by the boomerang-shaped epiplastron is obtuse and somewhat greater than 90 degrees in *muticus* (Fig. 17a); the angle of the epiplastron in *spinifer* and *ferox* is smaller than in *muticus* and forms an approximate right angle (Fig. 17b). Williams and McDowell (*op. cit.*:277, Pl. 1, Fig. 3) presented an illustration of the anterior plastral elements of an adult *T. ferox*. Siebenrock provided illustrations of the plastrons of *muticus* (*op. cit.*:823, Fig. 5) and *spinifer* (*op. cit.*:830, Fig. 10).

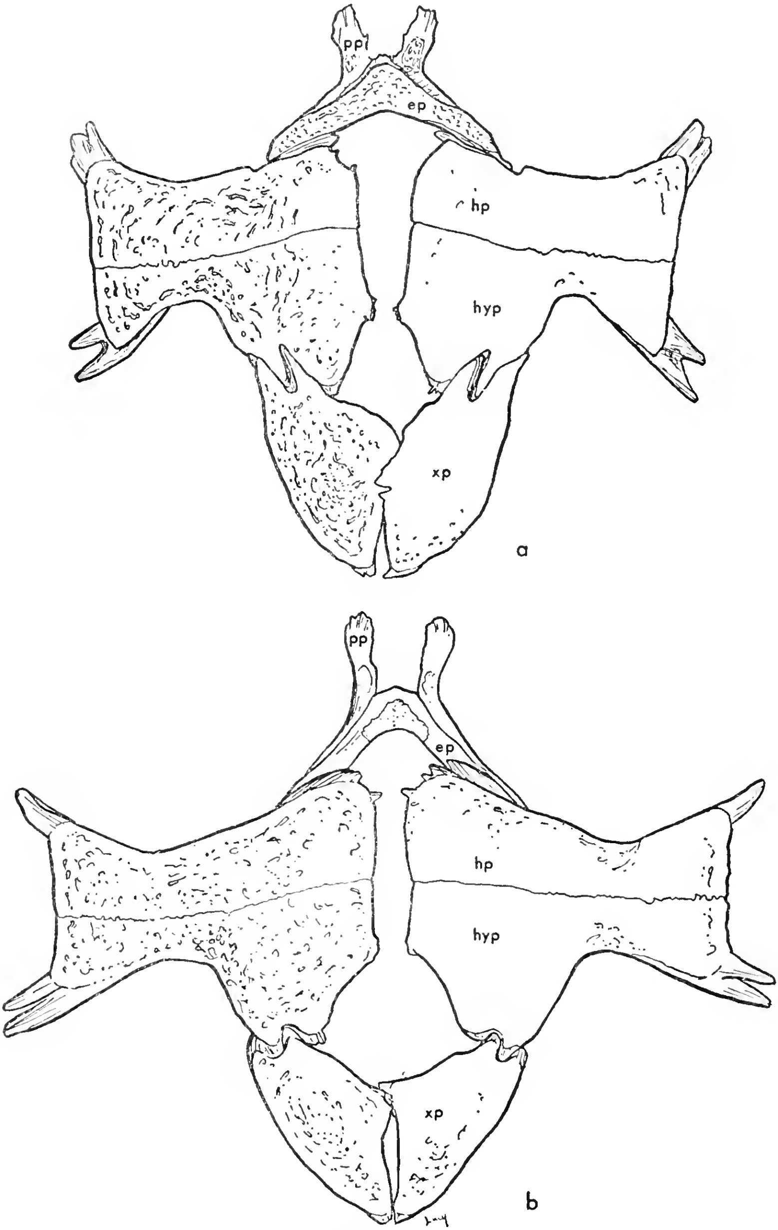


FIG. 17. Plastron of *Trionyx muticus* (a) and *T. spinifer* (b); sculpturing of callosities incompletely shown. ep, epiplastron; hp, hyoplastron; hyp, hypoplastron; pp, preplastron; xp, xiphiplastron. a—KU 1868, White River, Devall's Bluff, Prairie County, Arkansas (× ⅔); b—KU 1869, same locality (× ⅔).

Much importance has been credited to the fusion (no suture) or separation (suture present) of the hypoplastra and hyoplastra. The fusion of these bones distinguishes the genera *Lissemys, Cyclanorbis* and *Cycloderma* from *Trionyx, Pelochelys,* and *Chitra* (Siebenrock, *op. cit.*:815, 817; Loveridge and Williams, 1957:415). This character is also one of the criteria used by Hummel (1929: 768) in his erection of the two subfamilies Cyclanorbinae (= Lissemyinae) and Trionychinae. In my examination of specimens this character, unfortunately, was not given full attention. I have noted the fusion of the hypoplastra and hyoplastra in KU 1878 (*muticus,* right side only), KU 2219 (kyphotic *spinifer*), KU 16528 (*ferox*) and KU 60121 (*ferox*). Dr. Ernest E. Williams informs me in a letter of November 17, 1959, that of six specimens of *ferox* in the MCZ, the hyoplastra are fused with the hypoplastra in three (54689-90, 54686). I suspect that these bones in the three American species of the genus *Trionyx,* especially in *ferox,* fuse more often than is supposed.

In *muticus* the constricted part of the hyoplastron and hypoplastron is wider anteroposteriorly than in *spinifer* or *ferox* (Fig. 17).

The three American species have on the hyoplastra, hypoplastra, and xiphiplastra well-developed callosities, which enlarge with increasing size. The medial borders of the hyoplastral and hypoplastral callosities in larger specimens are rounded and closely approximated, often touching, as do the callosities of each xiphiplastron; seemingly, the callosities are relatively larger in *muticus* than in *spinifer* and *ferox.* I have seen one adult male *muticus* (KU 41380) that lacked median fontanelles or vacuities owing to the contact of the plastral elements (as viewed through overlying skin, alcoholic specimen). The bony plastron (approximately 9 cm. in maximal length) of a small *muticus* (KU 19460) resembles the plastron of larger individuals of *muticus* in having well-developed hyoplastral and hypoplastral callosities that are closely approximated medially. Large individuals of *muticus* usually have small, ovoid callosities on the preplastra, and a well-developed, angular callosity on the epiplastron (Fig. 17a). Siebenrock (*op. cit.*:823) suggests that the presence of callosities on the preplastra and epiplastron of *muticus* is subject to individual variation. I can not substantiate or dispute the supposition of Baur (1888:1122), Siebenrock (1924:193) and Stejneger (1944:12, 19) that the callosities are larger in males of *muticus* than in the females. Some individuals of *spinifer* have seven plastral callosities (KU 2842) as does *muticus,* but the callosities on the preplastra and epiplastron are less frequent and less well-developed in large specimens of *spinifer* than in *muticus.* The small epiplastral callosity in *spinifer* is located at the medial angle and does not extend posterolaterally to cover the entire surface of the epiplastron as it may in *muticus* (Fig. 17b). The epiplastron of a *spinifer* (KU 2826) has a medial callosity and another on the right posterolateral projection; three separate callosities occur on the epiplastron of MCZ 46615. The last specimen mentioned, a large, stuffed female, possesses a round, intercalary bone that tends to occlude the posteromedial vacuity. Seemingly, the callosity on the epiplastron appears prior to those on the preplastra; I have not seen any plastra having callosities on the preplastra and lacking a callosity on the epiplastron. I have not noted callosities on the preplastra or epiplastron of specimens of *ferox.*

The callosities on the plastral bones are sculptured; small, recently formed callosities on the preplastra and epiplastron lack sculpturing. The pattern of sculpturing on the plastral bones as well as that of the carapace is generally of anastamosing ridges. I am unable to discern any differences in pattern of sculpturing between the three American species. Stejneger distinguished adult specimens of *ferox* from the other American species by the coarseness of the sculpture of the bony callosities (1944:24) and of the bony carapace (*op. cit.*:32). The sculpturing on the plastral callosities and carapace seems to be correlated with size; larger specimens (*ferox*) have coarser sculpturing than do smaller specimens (*muticus*). Stejneger also mentioned that the sculpturing on many specimens of *ferox* is specialized into prominent, longitudinal welts (*loc. cit.*); these welts occur also on the carapace of *spinifer.*

On the basis of the osteological characters examined by me, *T. muticus* is distinguished from *spinifer* and *ferox* by a number of characters (plastron and especially skull) whereas the species *spinifer* and *ferox* are not easily distinguished from one another.

Composition of the Genus *Trionyx* in North America

Analysis of the characters previously mentioned and their geographic distribution permits the recognition of ten taxa, comprising four species and eight subspecies. Two subspecies, *T. spinifer pallidus* and *T. s. guadalupensis* are described as new. The four species and the included subspecies here recognized are:

Trionyx ferox	
Trionyx spinifer	*spinifer*
	hartwegi
	asper
	emoryi
	guadalupensis
	pallidus
Trionyx ater	
Trionyx muticus	*muticus*
	calvatus

The following key is designed to permit quick identification of living individuals; therefore, ratios and osteological characters are avoided as much as possible in favor of other characters that are the least variable and most "typical." Because there is considerable variation correlated with sex and size, each taxon occurs in the key in more than one couplet. Large females having mottled and blotched patterns will be the most difficult to identify. The characters listed should be used in combination because one character alone may not be sufficient; it is advisable to read both choices of each couplet. The text, figures and illustrations should be consulted for final identification.

ARTIFICIAL KEY TO NORTH AMERICAN SPECIES AND SUBSPECIES OF THE GENUS TRIONYX

1. Septal ridges present; tubercles on anterior edge of carapace present or absent 2

Septal ridges absent; anterior edge of carapace lacking tubercles or raised prominences 19

2. Plastral area a uniform dark slate or blackish; soft parts of body blackish having large pale marks dorsally; carapace having large black blotches, often fused along margin, on pale background, and many well-defined longitudinal ridges *T. ferox*, p. 479

Combination of characters not as above; ventral surface whitish, blackish flecks or blotches sometimes present 3

3\. Carapace having pattern of white dots, or black ocelli and/or spots; carapace sometimes gritty resembling sandpaper 4

Carapace uniform pale brownish or grayish, or having mottled and blotched pattern, contrasting or not; white dots or tubercles, black ocelli and/or spots may be present; carapace not gritty. 10

4\. Carapace having pattern of black ocelli and/or spots; numerous, conspicuous whitish spots or tubercles absent 5

Carapace having pattern of white dots that are sometimes surrounded by small black ocelli; small black dots may be interspersed among larger white dots 7

5\. Carapace having two or more marginal lines, these often diffuse and interrupted; black spots sometimes ocellate or bacilliform, or interspersed among smaller black dots; postocular and postlabial stripes usually united .... *spinifer asper,* p. 502

Carapace having only one dark marginal line; pattern of black ocelli or spots; postocular and postlabial stripes usually not united 6

6\. Carapace having prominent ocelli, which are much larger near the center than at the sides .... *spinifer spinifer,* p. 489

Carapace having numerous small, dark spots, sometimes small ocelli, which are not much larger near the center than the sides ....*spinifer hartwegi,* p. 497

7\. White spots on anterior third of carapace; white spots on carapace often surrounded by narrow blackish ocelli; small black dots sometimes interspersed among white spots. *spinifer guadalupensis,* p. 517

White spots absent on anterior third of carapace, or small and inconspicuous; white spots not surrounded by narrow blackish ocelli 8

8\. Pale rim of carapace narrow, partly obscured; overall dorsal coloration (including soft parts of body) dark and lacking pattern; few, small, white tubercles confined to posterior third of carapace .... *ater,* p. 528

Pale rim distinct, without markings; soft parts of body dorsally not uniformly dark; many white tubercles usually contrasting on pale carapace 9

9\. White spots confined to posterior third of carapace; ground color of carapace usually pale brown or tan, sometimes darker; a dark, slightly curved, line connecting anterior margins of orbits; postocular stripe usually interruped leaving pale, blotch behind eye; pale rim of carapace four or five times wider posteriorly than laterally .... *spinifer emoryi,* p. 510

Small white spots on posterior half of carapace gradually decreasing in size anteriorly, often indistinct or absent on anterior third of carapace; pale rim of carapace no more than three times wider posteriorly than laterally ...... *spinifer pallidus,* p. 522

10\. Marginal ridge present; carapace having ill-defined dark blotches on uniform grayish, lacking whitish tubercles or well-defined black spots or ocelli; pale rim of carapace absent; tubercles on anterior edge of carapace resembling flattened hemispheres; anterior parts of plastron often visible in dorsal view; postocular stripe, if present, having thick, blackish borders ..... *ferox,* p. 479

Marginal ridge absent 11

11\. Carapace uniform pale brownish, lacking mottled and blotched pattern, white dots, black ocelli or spots 12

Carapace having mottled and blotched pattern, contrasting or not; white spots or tubercles, black ocelli or spots may be present. 13

12. Pale rim of carapace four or five times wider posteriorly than laterally; dark, straight or slightly curved, line connecting anterior margins of orbits . . . . *spinifer emoryi,* p. 510

Pale rim of carapace no more than three times wider posteriorly than laterally . . . . *spinifer pallidus,* p. 522

13. Rear margin of carapace usually roughened by fine corrugations, edge often ragged; pale rim absent; carapace having dark brown-blackish, mottled and blotched pattern; anterior edge of carapace more or less smooth having scarcely elevated prominences; posterior part of plastral area and especially ventral surface of carapace having numerous black marks . . . . . . *ater,* p. 528

Rear margin of carapace smooth, edge entire; usually some evidence of pale rim **14**

14. White, rounded tubercles or spots usually evident posteriorly on carapace, sometimes indistinct; black ocelli or spots lacking in center of carapace, sometimes present at sides; shape of tubercles on anterior edge of carapace variable 15

White spots or tubercles absent; margin of carapace usually having black ocelli or spots; tubercles on anterior edge of carapace equilateral or conical, not low and flattened 17

15. White spots often present on anterior half of carapace; tubercles on anterior edge equilateral and wartlike, or less elevated, not conical . . . . *spinifer guadalupensis,* p. 517

White spots usually absent on anterior half of carapace, sometimes indistinct; shape of tubercles on anterior edge of carapace variable **16**

16. White spots absent on anterior half of carapace; tubercles on anterior edge of carapace low, scarcely elevated, never equilateral or conical; mottled and blotched pattern often not contrasting; ground color of carapace sometimes dark; pale rim of carapace four or five times wider posteriorly than laterally; dark, straight or slightly curved, line connecting anterior margins or orbits. *spinifer emoryi,* p. 510

White spots sometimes indistinct on carapace, or few, small spots present on posterior half of carapace; tubercles on anterior edge of carapace equilateral and wartlike or conical; mottled and blotched pattern usually contrasting; pale rim less than three times wider posteriorly than laterally . . . . . *spinifer pallidus,* p. 522

17. Carapace having evidence of more than one dark marginal line, and scattered, black spots or ocelli . . . . *spinifer asper,* p. 502

Carapace having only one, dark, marginal line 18

18. Carapace having small black spots, lacking large interrupted ocelli . . . . *spinifer hartwegi,* p. 497

Carapace having small black spots interspersed among larger, interrupted ocelli . . . . *spinifer spinifer,* p. 489

19. Carapace having pattern of dusky spots, sometimes short lines. 20

Carapace lacking pattern of dark spots or lines, having a mottled and blotched pattern 21

20. Pattern of circular spots, lacking short lines or bacilliform marks; spots sometimes slightly ocellate; no pale stripes on snout. *muticus calvatus,* p. 539

Pattern of dots, or dots and short lines; pale stripes on snout, at least just in front of eyes . . . . *muticus muticus,* p. 534

21. Mottled and blotched pattern usually contrasting; ill defined, blackish blotch absent behind eye . . . . . . *muticus muticus,* p. 534

Mottled and blotched pattern usually not contrasting; ill-defined, dark blotch may be present behind eye . . *muticus calvatus,* p. 539

Systematic Account of Species and Subspecies

Trionyx ferox (Schneider)

Florida Softshell

Plates 31 and 32

Testudo ferox Schneider, Naturg. Schildkr., p. 330, 1783 (based on Pennant, Philos. Trans. London, 61 (Pt. 1, Art. 32): 268, pl. 10 [figs. 1-3], 1772).

Trionyx ferox Schwartz, Charleston Mus. Leaflet, No. 26:17, pls. 1-3, May, 1956.

Testudo mollis Lacépède, Hist., Nat. Quadr. Ovip. Serp., 1:137, pl. 7, 1788.

Testudo (ferox?) verrucosa Schoepff, Hist. Testud., Fasc. 5 (Plag. M):90, pl. 19, 1795.

Testudo bartrami Daudin, Hist. Nat. Rept., 2:74, pl. 18, fig. 2, 1801.

Trionyx georgicus Geoffroy, Ann. Mus. Hist. Nat., Paris, 14:17, August, 1809.

Mesodeca bartrami Rafinesque, Atlan. Jour., Friend Knowledge, Philadelphia, 1 (No. 2, Art. 12):64, Summer, 1832.

Trionyx harlani Bell in Harlan, Medic. Phys. Research, p. 159, 1835.

Type.—Holotype, British Museum (Natural History) 1947.3.6.17; original number 53A, presumably that of Royal Society; stuffed adult female and skull; obtained from the Savannah River, Georgia, by Dr. Alexander Garden.

Range.—Southern South Carolina, southeastern Georgia, and all of Florida except the Keys and perhaps the western end of the panhandle (see map, Fig. 18).

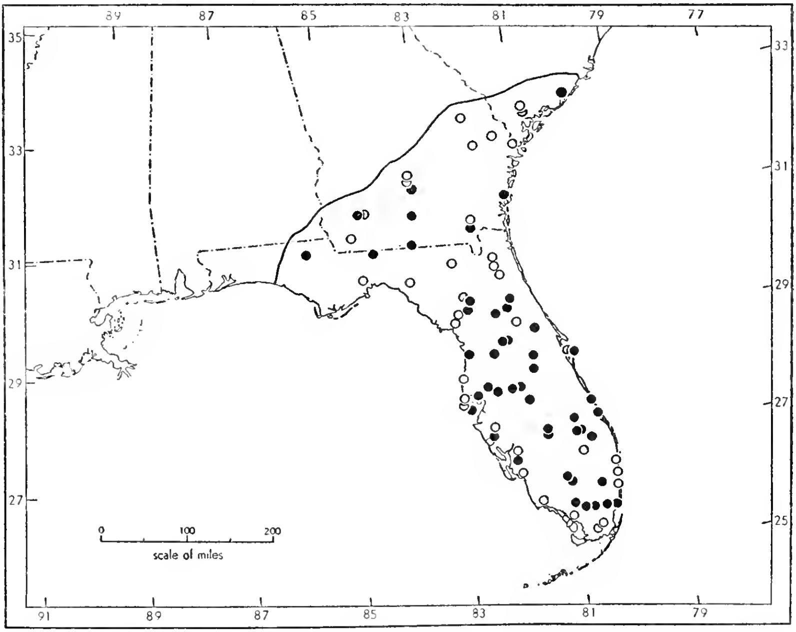


FIG. 18. Map of southeastern United States showing geographic distribution of *Trionyx ferox.*

Diagnosis.—Marginal ridge present; longitudinal rows of tubercles that resemble ridges on carapace of hatchlings; plastron often extending farther forward than carapace in adults; plastral area dark slate or gray in hatchlings; juvenal pattern of large slate or blackish blotches (often with pale centers) on a pale background; pale outer rim of carapace (absent on adults) narrow, not separated from ground color of carapace by distinct, dark line.

Size large; head wide; carapace relatively long and narrow; snout short; greatest width of skull at level of quadratojugal; often no suture between hypoplastra and hyoplastra; callosities on epiplastron and preplastra usually lacking.

Description.—Plastral length of smallest hatchling, 2.9 centimeters (UMMZ 95613), of largest male, 26.0 centimeters (AMNH 63642), of largest female, 34.0 centimeters (UMMZ 38123).

Septal ridges present; over-all coloration of carapace and plastron, and soft parts of body of hatchlings slate or blackish; carapace having blackish, circular blotches, usually fused at margin, often with pale centers on buff background forming coarse reticulum; pale, narrow rim of carapace not separated from ground color by dark marginal line; pale rim, coincident with marginal ridge, absent from anteriormost nuchal region; longitudinal rows of tubercles on carapace resembling ridges; undersurface blackish, usually having posterior part of carapace pale with irregular blackish marks; blackish soft parts of body dorsally having large, pale markings, most consistent of which are postocular mark that may contact orbit, postlabial mark that curves around angle of jaws, inverted Y on top of snout, and one or two streaks on side of neck.

Over-all coloration of adults grayish, paler than in hatchlings; carapace gray sometimes having slightly darker, large, irregular markings; mottled and blotched pattern on females not contrasting; sex of many large individuals not distinguishable on basis of pattern on carapace; pale rim of carapace obscure or absent; soft parts of body dorsally gray or brownish on large adults of both sexes, sometimes having slightly paler, large markings; small adult males usually having contrasting pattern on head; surface of carapace smooth (not "sandpaper") on adult males; undersurface whitish, throat often grayish; well-defined marginal ridge; anterior edge of carapace laterally to region of insertion of forelimbs studded with low, flattened tubercles resembling hemispheres, never conical; carapace usually having blunted tubercles, best developed anteriorly and posteriorly on midline, but sometimes linearly arranged, resembling ridges, especially at margins; anterolateral parts of plastron often extending farther forward than corresponding parts of carapace.

Range in length (in cm.) of plastron of ten largest specimens of each sex (mean follows extremes), males, 17.0-26.0, 20.0; females 23.3-34.0, 27.9; ontogenetic variation in PL/HW, mean PL/HW of specimens having plastral lengths 6.5 centimeters or less, 3.52, and exceeding 6.5 centimeters, 4.87; ontogenetic variation in CL/CW, mean CL/CW of specimens having plastral lengths 8.0 centimeters or less, 1.18, and exceeding 8.0 centimeters, 1.30; mean CL/PCW, 2.01; mean HW/SL, 1.44; mean CL/PL, 1.26.

Jaws of some skulls that exceed 75 millimeters in basicranial length having expanded alveolar surfaces; greatest width of skull usually at level of quadratojugal (72%); ventral surface of supraoccipital spine narrow proximally, usually having medial ridge; foramen magnum rhomboidal; opisthotic-exoccipital spur absent (82%), sometimes indicated by ridge (16%); distal part of opisthotic wing tapered, not visible in dorsal view; lateral condyle of articular surface of quadrate larger than medial articular surface, not tapered posteriorly; maxillaries in contact above premaxillaries; usually a combination of seven neurals, seven pairs of pleurals, and contact of seventh pair of pleurals (56%), often eight pairs of pleurals (31%); angle of epiplastron forming approximate right angle; often no suture between hypoplastra and hyoplastra; callosities on preplastra and epiplastron usually lacking.

Variation.—Crenshaw and Hopkins (1955:19) stated that in specimens from Lake Okeechobee and southward the carapace is wider relative to the width of the head, and Neill (1951:19) quoted Allen's observations that *ferox* from southern Florida "average larger and darker than those collected farther north."

Carr (1952:417) reported that the pale reticulum on the carapace is yellowish olive, the markings on head are yellow on an olive ground color, some markings more orange, and the plastron slate gray. Duellman and Schwartz (1958:271) mentioned that the carapace of hatchlings is edged in orange grading to yellow posteriorly and has a pattern of bluish-black blotches on a dull brown background, whereas the carapace is dull brown or blackish on adults. Neill (*op. cit.*:18) wrote "that the head stripes and the marginal ring of the 'carapace' are orange rather than yellow (yellow at the time of hatching, however)."

The transition from the dark coloration of hatchlings to the paler coloration of adults is gradual and subject to individual variation. The loss of dark color ventrally occurs first on the plastral area, then the hind limbs, forelimbs, posterior part of carapace and last on the neck and throat. The soft parts of the body dorsally are gray or dark gray, and do not become so pale as the ventral surface. The smallest specimen that I have seen displaying the dark features of the hatchlings is a male, 7.7 centimeters (UMMZ 100673); a female, 9.5 centimeters (UMMZ 110987), is the smallest specimen having a whitish plastral area. The change from dark to pale coloration on the ventral surface occurs at a size of 8.0 to 9.0 centimeters. The largest specimens I have seen having indistinct, dusky blotches of the underside of the carapace are a female, 11.3 centimeters (UMMZ 100836), and a male, 16.0 centimeters (UMMZ 106322). A contrasting pattern on head and limbs, and a dark throat are still evident in a female 19.2 centimeters (UMMZ 106302).

Comparisons.—*Trionyx ferox* can be distinguished from all other species of the genus in North America by the presence of a marginal ridge, longitudinal ridges of tubercles on the carapace of juveniles (less evident in adults), and the unique juvenal pattern and coloration. The lack of a juvenal pattern and a smooth surface on the carapace (not gritty like sandpaper) distinguish adult males from those of *T. spinifer.* Most adults of both sexes can be distinguished from *spinifer* and *muticus* by the extension of the plastron farther forward than the carapace (developed to a slight degree in some specimens of *T. s. emoryi*). Both sexes of all ages can be distinguished from *muticus* by the presence of knoblike tubercles on the anterior edge of the carapace, and septal ridges.

T. ferox is the largest species in North America; the maximum size of the plastron in adult males is approximately 26.0 centimeters (16.0 in *spinifer*) and of adult females, 34.0 centimeters (31.0 in *spinifer*). The head is wider in *ferox* than in *muticus* and most subspecies of *spinifer* (closely approached by *asper, guadalupensis, emoryi* and *T. ater*). The carapace is narrower in *ferox* than in *muticus* and most subspecies of *spinifer* (closely approached by *emoryi* and *T. ater*). The snout is shortest in *ferox*, but almost as short in *T. s. emoryi* and *T. ater*. *T. ferox* has proportionately the longest plastron in relation to length of carapace.

Most skulls of *ferox* differ from those of *muticus* and *spinifer* in having the greatest width at the level of the quadratojugal (as do some *T. s. asper;* see account of that subspecies). In the skull, *ferox* resembles *spinifer* but differs from *muticus* in having the 1) ventral surface of the supraoccipital spine narrow proximally, and usually having a medial ridge, 2) foramen magnum rhomboidal, 3) distal part of opisthotic wing tapered, 4) lateral condyle of articular surface of quadrate not tapered posteriorly, and larger than medial articular surface, and 5) maxillaries in contact above premaxillaries. *T. ferox* resembles *muticus* but differs from most individuals of *spinifer* in lacking a well-developed opisthotic-exoccipital spur. *T. ferox* resembles *spinifer* but differs from *muticus* in having the epiplastron bent at approximately a right angle; *ferox* differs from both *muticus* and *spinifer* in lacking a callosity on the epiplastron and probably in the more frequent fusion of the hyoplastra and hypoplastra.

Remarks.—The early taxonomic history of *Trionyx ferox* has been discussed in detail by Stejneger (1944:27-32), who explained that Dr. Alexander Garden of Charleston, South Carolina, sent a description and specimen of *T. ferox* to Thomas Pennant, and at the same time sent another specimen with drawings to a friend, John Ellis, in London. Pennant presented one of the specimens and drawings and the description to the Royal Society of London in 1771; the description was published in 1772 and included Garden's drawings. Because two specimens were involved the possibility exists that the description (text, drawings and type specimen) is a composite based on two specimens.

I have not seen the type. Garden's original description (in Pennant, 1772: 268-271) leaves little doubt that the text subject is a large adult female of *ferox* (see especially the statements, "fore part, [of carapace] just where it covers the head and neck, is studded full of large knobs. [and] The under, or belly plate, . . . is . . . extended forward two or three inches more than the back plate, . . ."). I am indebted to Mr. J. C. Battersby, British Museum (Natural History), Department of Zoology (Reptiles), for information concerning the type and for comparing it with the text description and three figures published by Pennant. The carapace of the type is approximately 16 inches long, 13½ inches wide, and has low, flattened, knoblike tubercles along the anterior edge. Some inaccuracies on the part of the artist (such as five claws on both feet on the right side of Fig. 3, and four claws on the left front foot of Fig. 2 are evident), and slight changes in the proportions of the type would have occurred after death and preservation. It is the opinion of Mr. Battersby that the type, text description and three figures represent one specimen. Figures 1 and 2, dorsal and ventral views respectively, probably represent the same specimen from life; the neck is withdrawn and the tail tip is visible in dorsal view, but concealed beneath the posterior edge of the carapace in ventral view. Presumably the same specimen (probably drawn from dried and stuffed animal) is depicted in Figure 3 (dorsal view); the neck is fully extended and a large part of the thick, pyramidal tail is visible in dorsal view. British Museum (Natural History) 1947.3.6.17 is considered a holotype. The three figures published by Pennant have been duplicated by Schoepff (1795:Pl. 19) and Duméril and Bibron (1835:482). To my knowledge, the holotype was first specifically designated as the "(Type.)" of *T. ferox* by Boulenger (1889:259). The skull of the holotype is figured by Stejneger (1944:Pl. 5).

Garden did not list a specific locality for the two specimens that he sent to London, but did mention that the turtle was common in the Savannah and Altamaha rivers (of Georgia), and rivers in east Florida. Boulenger (*loc. cit.*) stated that the locality of the holotype was "Georgia." Baur (1893:220) restricted the type locality to the "Savannah river, Ga." Neill (1951:17), who believed *T. ferox* to be absent from the Savannah River, changed the type locality of *ferox* to east Florida. Schwartz (1956:8) reappraised the status of softshells in Georgia and Florida and reëstablished the Savannah River (at Savannah), Georgia, as the type locality of *T. ferox*.

Pennant failed to use binomial nomenclature when he published the type description of Garden. The first name-combination (*Testudo ferox*) was proposed by Schneider (1783:220).

Lacépède (1788:137, Pl. 7) referred to Garden's description in Pennant only as "The Molle" but on a folded paper chart entitled "Table Méthodique des Quadrupèdes ovipares," which is inserted after an introduction of 17 pages, listed *T. mollis*; this name is again listed on another folded chart, entitled "Synopsis methodica Quadrupedum oviparorum," which is inserted between pages 618 and 619 under the genus *Testudo*. The illustration (Pl. 7) was taken from Pennant (Duméril and Bibron, *loc. cit.*). The type locality has been designated "(following Stejneger, 1944) as eastern Florida" by Schmidt (1953:108).

Bartram failed to use a binomial name with his description of "the great soft shelled tortoise," which appeared in his *Travels* (1791:177-179, Pl. 4 and unnumbered plate between pages 282 and 283) and two editions of a French translation (1799 and 1801, 1:307); see Harper (1940). Recently, Bartram's *Travels* has been placed on the Official Index of Rejected and Invalid Works in Zoological Nomenclature, Opinion 447 (see Hemming, 1957). Bartram's description of a soft-shelled turtle has provided the basis for the proposal of at least three name-combinations. The first was *Testudo (ferox?) verrucosa* proposed in 1795 by Schoepff; it appeared simultaneously in *The Historia Testudinum* and in a German translation, *Naturgeschichte der Schildkröten* (see Mittleman, 1944:245). Stejneger (1944:26) listed the type locality as eastern Florida. Daudin (1801:74), also referring to Bartram's description in his *Voyage* (French translation), proposed the name *Testudo bartrami*; Harper (*op. cit.*:717) restricted the type locality of *T. bartrami* from "Half-way pond," east Florida, to southwestern Putnam County between Palatka and Gainesville, Florida. Rafinesque (1832:64-65), relying on the authenticity of the illustrations in Bartram's *Travels* that depict a soft-shelled turtle having five claws on each of the hind feet, tubercles on the sides of the head and neck, and ten scales in the middle of the carapace (presumably inaccuracies or a composite on the part of the artist), referred to Bartram's description as a new genus, *Mesodeca bartrami*, a name which Boulenger (1889:245, footnote) referred to as "mythical." Geoffroy (1809a:18-19) considered Bartram's description the basis for the recognition of a second species of *Chelys* (binomial nomenclature not employed), and Duméril and Bibron (*loc. cit.*) suggested that the description was based partly on a "Chelyde Matamata."

The descriptive comments of Bartram are not clearly applicable to *Testudo ferox* Schneider; *Trionyx ferox*, however, is the only species of soft-shelled turtle known to occur in the region of Bartram's observations (east Florida), and the type locality was restricted to Putnam County, Florida, by Harper. The name-combinations, *Testudo (ferox?) verrucosa* Schoepff, *Testudo bartrami* Daudin, and *Mesodeca bartrami* Rafinesque are junior synonyms of *Testudo ferox* Schneider.

Schweigger (1812:285) referred *ferox* to the genus *Trionyx* following the description of that genus by Geoffroy in 1809. *Testudo ferox* was listed as a synonym by Geoffroy in the description of *Trionyx georgicus* (1809a:17); Duméril and Bibron (1835:432) mentioned that the specific characters of *georgicus* were taken from Pennant. The name *Trionyx georgianus* presumably appears for this taxon in Geoffroy's earlier-published synopsis (1809:367). *T. georgicus* was listed as occurring in rivers of Georgia and the Carolinas; the type locality was restricted by Schmidt (*op. cit.*:109) to the Savannah River, Georgia. The two specific names *georgicus* and *georgianus* are regarded as substitute names and junior synonyms of *T. ferox*.

Geoffroy (1809a:14-15) also described *Trionyx carinatus*, a name-combination that hitherto has been considered a synonym of *Trionyx ferox*. There is no indication from the description that *carinatus* is applicable to *ferox*. Most comments pertain to a description of the bony carapace and plastron, which Geoffroy depicts in Plate 4. It is a young specimen judging from the small and isolated preneural; the seventh pair of pleurals is unusual in being fused (no middorsal suture), and the neurals seem large in proportion to the size of the pleurals. The anterior border of the carapace is described as having tubercles. Geoffroy listed *Testudo membranacea* and *Testudo rostrata* as synonyms of *carinatus*. Fitzinger (1835:127) listed *T. membranacea*, *T. rostrata* and *T. carinatus* as synonyms of *Trionyx javanicus* (= *T. cartilagineus*), which was also described by Geoffroy (*op. cit.*:15). Duméril and Bibron (*op. cit.*:478, 482) considered *carinatus* to be the young of *spinifer* (*ferox* as synonym). Gray (1844:48), however, referred *T. membranacea* and *T. rostrata* to the synonymy of *T. javanicus*, but considered *T. carinatus* to be a synonym of *T. ferox* (*op. cit.*:50), an interpretation followed by all subsequent authors. *Trionyx carinatus* is questionably listed as a synonym of *ferox* by Stejneger (1944:27). Duméril and Bibron (*op. cit.*:482) wrote that the young type of *carinatus* is in the museum at Paris. Dr. Jean Guibé informs me in letter of September 24, 1959, that the type of Geoffroy's *T. carinatus* cannot be found in the Natural History Museum at Paris. For the present, *T. carinatus* is considered a *nomen dubium*. According to Stejneger (1944:27), *Trionyx brongniarti* Schweigger is a substitute name for *T. carinatus*.

I am unable to add anything to Stejneger's (*op. cit.*:32) account of *Trionyx harlani;* the mention of its occurrence in east Florida indicates that it is indistinguishable from *Testudo ferox* Schneider.

T. ferox was considered to be indistinguishable from Lesueur's *Trionyx spiniferus* (described in 1827), until Agassiz (1857:401) pointed out the differences between the two species. However, Agassiz (*op. cit.*:402, Pl. 6, Fig. 3) regarded juveniles of *T. spinifer asper* as the young of *ferox*. Consequently, the geographic range of *ferox*, as envisioned by Agassiz, extended from Georgia and Florida west to Louisiana. Neill (1951:15) considered all

American forms conspecific. Crenshaw and Hopkins (1955) and Schwartz (1956) demonstrated that *ferox* is a distinct species.

Fitzinger (1843:30) designated the species *ferox* as the type species of his genus *Platypeltis* as follows: "Platypeltis. Fitz. Am[erica]. *Platypelt. ferox*. Fitz. Typus." If populations of soft-shelled turtles that are referable to *Testudo ferox* Schneider are considered to comprise a distinct genus by future workers, *Platypeltis* Fitzinger, 1835, is available as a generic name with *Testudo ferox* Schneider, 1783, as the type species (by subsequent designation).

Trionyx ferox in the northern part of its range is sympatric with *T. spinifer asper*. In the region of overlap, the two species are nearly always ecologically isolated; *ferox* inhabits lentic waters, whereas *T. s. asper* is partial to lotic waters (Crenshaw and Hopkins, *op. cit.*:16). There is no evidence of intergradation or hybridization.

Many characters of *Trionyx ferox* that are lacking in other North American forms are shared with some Asiatic softshells, such as the large size, longitudinal rows of tubercles that resemble ridges on the carapace, and the marginal ridge. It is thought that, of the living softshells in North America, *ferox* is more closely allied to Old World forms of the genus than to *muticus* or *spinifer*.

Carr (1940:107) recorded *ferox* from Okaloosa County, Florida, in the western end of the panhandle, whereas Crenshaw and Hopkins (1955:16) list the known westward extent of range as Leon and Wakulla counties. AMNH 6933 from west of the Apalachicola drainage in Washington County, Florida, tends to substantiate Carr's record, which is not included on the distribution map.

Specimens examined.—Total 144, as follows: Florida: *Alachua:* UMMZ 64178, 100969; USNM 10545, 10704, "near" Gainesville; UMMZ 56599, Levy Lake. *Brevard:* AMNH 12878, Canaveral. *Broward:* UMMZ 109441, Hugh Taylor Birch State Park; USNM 109548, 22 mi. WNW, 6 mi. SSE Fort Lauderdale. *Collier:* USNM 86828, Tamiami Trail, "near" Birdon. *Dade:* AMNH 50936, UMMZ 10183, 110981, Miami; USNM 84079, 86942, 15 mi. from (west) Miami, Tamiami Trail; UMMZ 111371, 19 mi. W, 1.3 mi. S Miami; UI 28984, 35 mi. W. (Miami) Tamiami Trail; AMNH 69932-33, UMMZ 101582, 101584, 104024, 40-45 mi. W Miami, Tamiami Trail. *Glades:* UMMZ 100836, mouth of Kissimmee River. *Hendry:* UMMZ 106302, 10.2 mi. SE Devil's Garden; UMMZ 106303-04, 106321-22, 30 mi. S Clewiston, near Devil's Garden. *Hernando:* TU 13624, 0.5 mi. S Citrus Co. line on US Hwy. 19. *Highland:* AMNH 65537, 71618, Archbold Biol. Stat., Lake Placid; AMNH 65622, Hicoria. *Hillsborough:* TU 13960, Hillsborough River, *ca.* 20 mi. NE Tampa; USNM 51184, Tampa; USNM 71156, Plant City. *Indian River:* USNM 55316, Vero Beach; USNM 59318, Sebastian. *Lake:* UMMZ 36072, USNM 20189, 029210, 029339, 38123, Eustis; UMMZ 76754-56, Lake Griffin. *Lee:* UMMZ 102276, 14 mi. SE Punta Gorda. *Leon:* CNHM 33701, USNM 95767, Lake Iamonia; USNM 103736, Silver Lake. *Marion:* AMNH 8294-95, UMMZ 95613 (4), USNM 52476-83, 100902-04, Eureka; AMNH 63642, near Salt Springs. *Martin:* TNHC 1292, 8.4 mi. N Port Mayaca. *Okeechobee:* AMNH 57379-84, Lake Okeechobee; AMNH 5931-32, Kissimmee Prairie. *Orange:* USNM 51421, 56805, Orlando; KU 16528. *Osceola:* USNM 029448, 029450-64, 029467-68, 029470, 029474-75, Kissimmee. *Palm Beach:* UMMZ 54101, Palm Beach; USNM 73199, Delray Beach. *Pinellas:* USNM 51417-20, St. Petersburg. *Polk:* AMNH 25543, Lakeland; UMMZ 112380, 6.7 mi. S Lake Wales; USNM 60496, 60532, 60534, 61083-87, Auburndale. *Putnam:* USNM 4373, 7651, Palatka; USNM 26035, ponds "near" Welaka. *Sarasota:* USNM 61352, Lake Myakka. *Sumpter:* UMMZ 71791, Bushnell. *Volusia:* UMMZ 100673, Lake Helen. *Washington:* AMNH 6933, Washington. *County unknown:* AMNH 4758; USNM 8899, St. John's River: USNM 59727-28, Lake Okeechobee, "near" mouth Taylor's Creek; USNM 84080.

Georgia: *Baker:* SM 2083, USNM 029619, 38980-81, 70398, Mimsville.

Berrien: USNM 62217, Banks Mill Pond. *Charlton:* AMNH 69934, Okefinokee Swamp, SW Billy's Island; UMMZ 90010, east edge Okefinokee Swamp; USNM 84603, Okefinokee Swamp, Chesser's Island. *Irwin:* USNM 56804. *Lowndes:* UMMZ 67706, 10 mi. S Valdosta. *McIntosh:* USNM 19621, Darien.

SOUTH CAROLINA: *Charleston:* USNM 9670, Charleston.

NO DATA: AMNH 22750; USNM 71608-09.

Records in the literature.—FLORIDA: *Alachua:* 10 mi. ENE Gainesville (Schwartz, 1956:18). *Brevard:* Merritt Island (Neill, 1958:6). *Broward:* Fort Lauderdale (Schwartz, *op. cit.*:19). *Charlotte:* (Carr, 1940:107). *Clay:* Green Cove Springs (Brimley, 1910:18); St. John's River (Crenshaw and Hopkins, 1955:21); Doctor's Inlet (Schwartz, *op. cit.*:18). *Collier:* Royal Palm Hammock (Crenshaw and Hopkins, *op. cit.*:20); 11.2 mi. E Monroe Station (Schwartz, *op. cit.*:19). *Columbia:* (Carr, *loc. cit.*). *Dade:* Paradise Key (Schwartz, *loc. cit.*); Homestead (eggs, Stejneger, 1944:43). *Duval:* 4-10 mi. S Jacksonville (Deckert, 1918:31). *Glades: ca.* 8 mi. SW Okeechobee State Park. *Lake:* Alexander Springs (Schwartz, *op. cit.*:18). *Lee:* 18 mi. S Fort Myers (Conant, 1930:63); 6 mi. SE Fort Myers (Hamilton, 1947:209). *Levy:* Gulf Hammock (Schwartz, *loc. cit.*); Brownson (Stejneger, *op. cit.*:42). *Monroe* and *Okaloosa* (Carr, *loc. cit.*). *Okeechobee:* 6 mi. E Kissimmee River; state hwy. 78 "near" Okeechobee-Glades co. line. *Palm Beach:* SW part of Lake Okeechobee, near Clewiston; Milton Island Cove (Schwartz, *loc. cit.*). *Pasco:* mouth Pithlachascotee River (Neill, *op. cit.*:26). *Pinellas:* Belleair (Brimley, *loc. cit.*); Seminole (Conant, *loc. cit.*); 5 mi. E Clearwater (Schwartz, *op. cit.*:19); Gulf Port (Stejneger, *op. cit.*:43). *Polk:* Lake Shipp, near Winter Haven (Telford, 1952:185). *Sarasota:* 15 mi. E Sarasota (Conant, *loc. cit.*); Venice (Conant, *op. cit.*:61). *Taylor:* "near" Foley. *Wakulla:* "near" Crawfordville (Crenshaw and Hopkins, *op. cit.*:15).

GEORGIA: *Baker:* 5 mi. NW Newton, 5 mi. W Newton, 4 mi. N Newton. *Ben Hill:* 6 mi. E Fitzgerald (Crenshaw and Hopkins, 1955:15). *Bulloch:* 14 mi. SE Statesboro (Schwartz, 1956:19). *Decatur:* "near" Bainbridge (Crenshaw and Hopkins, *loc. cit.*). *Emanuel:* "near" Midville. *Evans:* 8 mi. NE Manassas, Tattnall County. *Ware:* Laura Walker State Park (Schwartz, *loc. cit.*). *Wilcox:* 3 mi. SE Forest Glen (Crenshaw and Hopkins, *op. cit.*:19).

SOUTH CAROLINA: *Beaufort:* 7 mi. NE Gardens Corner (Schwartz, 1956:19). *Chatham:* Savannah River at Savannah (Schwartz, *op. cit.*:8-9). *Colleton:* 5 mi. from Whitehall, Combahee River (Schwartz, *op. cit.*:19).

Trionyx spinifer Lesueur

Spiny Softshell

Range.—In Canada, southern Ontario and Quebec; in the United States, northwestern Vermont and western New York south to northern Florida, east to central Montana, eastern Wyoming and Colorado, and New Mexico; introduced into the Colorado River system of California, Nevada, Arizona and New Mexico; in México, the northern part of the states of Tamaulipas, Nuevo León, Coahuila, and eastern Chihuahua (see map, Fig. 19).

Diagnosis.—Juvenal pattern uniform tan or brownish lacking markings, having whitish dots or spots, or having well-defined, blackish ocelli or spots; surface of carapace "sandpapery" in adult males; conical projections (in some subspecies) along anterior edge of carapace in large females; contrasting pattern of blackish marks on pale background (in some subspecies) on dorsal surface of limbs of adult males.

Opisthotic-exoccipital spur well-developed; epiplastral callosity, when present, not covering entire surface.

Description.—Septal ridges present; external and proportional characteristics variable (see accounts of subspecies); range in length of plastron (cm.) of ten

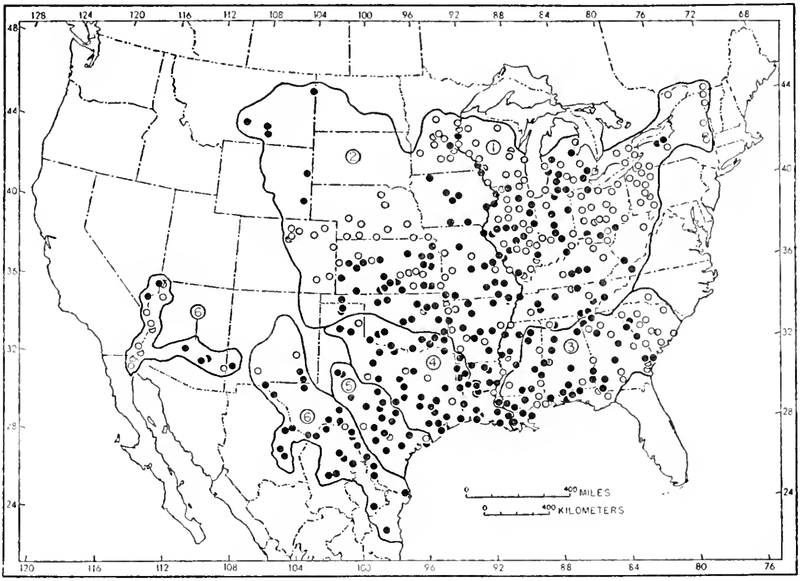


FIG. 19. Geographic distribution of *Trionyx spinifer*.

Guide to subspecies:

1. *T. s. spinifer*
2. *T. s. hartwegi*
3. *T. s. asper*
4. *T. s. pallidus*
5. *T. s. guadalupensis*
6. *T. s. emoryi*

largest specimens of each sex (mean follows extremes), males, 13.8-16.0, 14.4; females, 26.0-31.0, 28.0.

Greatest width of skull usually at level of squamosal (74%); foramen magnum rhomboidal; ventral surface of supraoccipital spine narrow proximally, usually having medial ridge; opisthotic-exoccipital spur well-developed (66%); distal part of opisthotic wing tapered, not visible in dorsal view; lateral condyle of articular surface of quadrate larger than medial articular surface, not tapered posteriorly; maxillaries in contact above premaxillaries (88%); usually a combination of seven neurals, seven pairs of pleurals and contact of seventh pair of pleurals (83%); angle of epiplastron approximately 90 degrees; callosities when present on epiplastron not covering entire surface; hyo-hypoplastral suture usually present.

Comparisons.—Trionyx spinifer can be distinguished from *T. ferox* and *T. muticus* by the presence of any one of the characters mentioned in the "Diagnosis." Both sexes and all sizes of *T. spinifer* resemble *ferox* but differ from *muticus* in having septal ridges. Most individuals of *T. spinifer* (except some large females) resemble *muticus* but differ from *ferox* and large females of *ater* in having a pale outer rim that is separated from the ground color of the carapace by a distinct (*spinifer*) or dusky (*muticus*) dark line. Large females of the subspecies *spinifer, hartwegi, asper* and *pallidus* may have enlarged conical projections along the anterior edge of the carapace and, unless these projections are considerably worn, are readily distinguished from large females of *ferox* (flattened, knoblike prominences), and *muticus* and *ater* (smooth surface, no prominences). Large females of the subspecies *guadalupensis* and *emoryi* resemble *muticus* and *ater,* and to some extent *ferox,* in having low, scarcely elevated prominences along the anterior edge of the carapace. Some females of *emoryi* resemble *ferox* in that the plastron extends farther forward than the carapace.

T. spinifer is intermediate in size between *ferox* (larger) and *muticus* (smaller); the maximum size of the plastron in adult males is approximately 16.0 centimeters (14.0, *muticus*; 26.0, *ferox*), and of females, 31.0 centimeters (21.5, *muticus;* 32.5, *ferox*). The head for all subspecies of *spinifer* is proportionately narrower than in *ferox* but wider than in *muticus.*

In the skull, *spinifer* more closely resembles *ferox* than *muticus,* but differs from both *ferox* and *muticus* in usually having a well-developed opisthotic-exoccipital spur. Skulls of *spinifer* resemble those of *muticus* but differ from those of *ferox* in being widest at the level of the squamosal. Skulls of *spinifer* resemble those of *ferox* but differ from those of *muticus* in having the 1) ventral surface of the supraoccipital spine narrow proximally, and usually having a medial ridge, 2) foramen magnum rhomboidal, 3) distal part of opisthotic wing tapered; 4) lateral condyle of articular surface of quadrate not tapered posteriorly, and larger than medial articular surface, and 5) maxillaries in contact above premaxillaries. *T. spinifer* resembles *ferox* but differs from *muticus* in having the epiplastron bent at an approximate right angle. *T. spinifer* differs from *ferox* in having an epiplastral callosity, and from *muticus* in that the callosity does not cover the entire surface of the epiplastron. The hyo-hypoplastral suture is present more often in *spinifer* and *muticus* than in *ferox.*

Remarks.—Gray (1869:221) proposed the generic name *Callinia* as a new name for *Aspidonectes* as understood by Agassiz (1857:403). Gray referred *Trionyx spiciferus* (= *spiniferus*) Lesueur to *Callinia.* Stejneger (1907:514) designated *Trionyx spiniferus* Lesueur as the type species of *Callinia.* If *Trionyx spiniferus* Lesueur is considered to be generically distinct from other soft-shelled turtles, *Callinia* Gray, 1869, is available as a generic name with *Trionyx spiniferus* Lesueur, 1827, as the type species by subsequent designation.

Geographic variation.—*T. spinifer* is the most variable and widespread species of the genus in North America. Size of ocelli on the carapace decreases from east to west on turtles inhabiting waterways of the Upper Mississippi River drainage. The most impressive gradient, geographically oriented from western Louisiana to southwestern Texas is seen in each of several features: decrease in size of tubercles on the anterior edge of the carapace, reduction in contrast of pattern on the dorsal surface of limbs and side of head, change in pattern on the dorsal surface of the snout, and increase in the size of white spots on the carapace. But the gradient in size of white spots is reversed in *T. s. emoryi,* which has small white spots on the carapace. Some of the characters at the western terminus of this geographical gradient are shared with

T. ater and *muticus.* Those subspecies comprising the *emoryi* group also show proportional characters that correspond closely with those of *T. ferox.*

On the basis of tuberculation and pattern on carapace, side of head, dorsal surface of limbs and snout, *Trionyx spinifer* may be divided into six subspecies.

Trionyx spinifer spinifer Lesueur

Eastern Spiny Softshell

Plates 33, 34, and 52

Trionyx spiniferus Lesueur, Mém. Mus. Hist. Nat. Paris, 15:258, pl. 6, December, 1827.

T[rionyx] s[pinifer] spinifer Schwartz, Charleston Mus. Leaflet, No. 26:11, May, 1956.

Trionyx ocellatus Lesueur, Mém. Mus. Hist. Nat. Paris, 15:261, December, 1827.

Apalone hudsonica Rafinesque, Atlan. Jour., Friend Knowledge, Philadelphia, 1(No. 2, Art. 12):64, Summer, 1832.

Trionyx annulifer Wied-Neuwied, Riese Nord-Amerika, 1(pt. 3):140, 1838.

Tyrse argus Gray, Cat. Tort. Croc. Amphis. Brit. Mus., p. 48, 1844.

Aspidonectes nuchalis Agassiz, Contr. Nat. Hist. United States, 1(pt. 2):406, 1857.

?*G[ymnopus] olivaceus* Wied-Neuwied, Nova Acta Acad. Leopold.-Carol., 32:55, pl. 5, 1865.

Type.—Lectotype, Museum d'Histoire Naturelle, Paris, No. 8808; large stuffed female obtained by C. A. Lesueur from the Wabash River, New Harmony, Posey County, Indiana (Pl. 52).

Range.—Northeastern United States and extreme southeastern Canada in tributaries flowing into the Mississippi River from the east, and the St. Lawrence River drainage; extreme southern Quebec and Ontario, Canada, east through southern Great Lakes region to Wisconsin, and south through New York, western Pennsylvania and Illinois to Tennessee and western Virginia (see map, Fig. 19).

Diagnosis.—Juvenal pattern of large, thick-bordered black ocelli, often 9-10 millimeters in diameter in center of carapace on adult males, and 2-3 millimeters in diameter on hatchlings (mean OD/PL, Michigan, .066); only one dark marginal line separating pale rim of carapace from dorsal ground color.

Description.—Plastral length of smallest hatchling, 2.7 centimeters (UMMZ 89950, INHS 3143); of largest male, 14.5 centimeters (UMMZ 72512); of largest female, 31.0 centimeters (UMMZ 40866).

Carapace olive, having large ocelli in center but smaller ocelli or spots at sides; ocelli often interrupted; pale rim of carapace not four or five times wider posteriorly than laterally, separated from darker ground color of carapace by one dark marginal line; large females often having remnants of ocelli at sides of carapace on mottled and blotched background; pattern on snout of pale, dark-bordered stripes that unite forming acute angle in front of eyes; well-defined dark markings in subocular and postlabial region; pattern contrasting with ground color on side of head; postlabial stripe interrupted, diffuse; pale postocular stripe having blackish borders interrupted, not uniting with postlabial stripe; dorsal surface of soft parts of body having contrasting pattern, largest blackish marks on hind limbs; elongate tail of adult males having pale dorsolateral bands with well-defined lower blackish borders; underparts whitish, often having blackish marks, except in center of plastral area; dark marks on webbing of limbs, palms and soles; dark streaks often coincident with digits; small conical tubercles on anterior edge of carapace on adult males; conical or equilateral tubercles on anterior edge of carapace of large females; accessory knoblike tubercles in nuchal region and in middle of carapace posteriorly on large females.

Ontogenetic variation in PL/HW, mean PL/HW of specimens having plastral lengths 7.0 centimeters or less, 4.09, and exceeding 7.0 centimeters, 5.50; ontogenetic variation in CL/CW, mean CL/CW of specimens having plastral lengths 8.5 centimeters or less, 1.12, and exceeding 8.5 centimeters, 1.21; mean CL/PCW, 2.02; mean HW/SL, 1.30 (including subspecies *hartwegi*); mean CL/PL, 1.39.

Variation.—Variant individuals include: UMMZ 72512, an adult male, having some ocelli seven millimeters in diameter that are almost solid spots; UMMZ 89659 having postocular and postlabial stripes connected on right side of head; UMMZ 95615, 52948, 54402 having inner dark borders of pale stripes on snout represented by short dashes and dots (a ragged line connecting anterior margins of orbits on 54402); UMMZ 52948, 89659 having interrupted, black marginal lines on carapace with ends of some segments oriented inward and overlapping portion of adjacent segments; UMMZ 81699, female having plastral length of 19.0 centimeters, lacking conspicuous tubercles on anterior edge of carapace; UI 2403, CNHM 92204 having extensive dark mottling and marbling on throat and neck, undersurface of limbs and posterior portion of carapace.

Comparisons.—*T. s. spinifer* can be distinguished from all other subspecies of *T. spinifer* by the presence of large black ocelli (diameter 9-10 mm. on adult males, 2-3 mm. on hatchlings) in combination with only one dark marginal line. *T. s. spinifer* resembles *asper* in having ocelli or dots on the carapace but differs from *asper* in having only one dark marginal line and larger ocelli. *T. s. spinifer* differs from *hartwegi* only in the large size of the ocelli. *T. s. spinifer* resembles *hartwegi* and *asper* but differs from *pallidus, guadalupensis* and *emoryi* in having blackish spots and ocelli on the carapace and lacking whitish dots. *T. s. spinifer* resembles *hartwegi, asper,* and *pallidus* and differs from *guadalupensis* and *emoryi* in having conical or knoblike tubercles on the anterior edge of the carapace on large females.

T. s. spinifer differs from the subspecies *asper, guadalupensis* and *emoryi* in having a relatively narrower head, and from *emoryi* in having a relatively wider carapace. *T. s. spinifer* resembles *hartwegi* and *asper* but differs from the other subspecies in having the carapace widest at a plane approximately one-half way back on the carapace. The subspecies *spinifer* and *hartwegi* have longer snouts than *pallidus, guadalupensis,* and *emoryi*. *T. s. spinifer* differs from *asper* but resembles all the other subspecies in having a relatively longer plastron.

Remarks.—Lesueur's description of *Trionyx spiniferus* (1827:258-261, Pl. 6) seems to be based mostly, if not entirely, on a large female (length of carapace, 13 inches), which was "Le plus grand des individus observes . . ."

(*op. cit.*:258); an accompanying illustration depicting the dorsal surface of the bony carapace is unusual in lacking neurals (Pl. 6, E). Duméril and Bibron (1835:481) mentioned eight or nine additional specimens that Lesueur sent to the Museum of Natural History in Paris. Dr. Jean Guibé informed me under letter dated September 24, 1959, that a larger stuffed female, bearing catalog number 8808 is regarded as the holotype, and that there are seven additional specimens (1949, 4143, 8807, 8809-12) in the museum at Paris. All turtles were obtained by Lesueur from the Wabash River. To my knowledge no specimen that was available to Lesueur has been specifically designated as a type. Because the description seems to be based on one specimen, undoubtedly No. 8808, this specimen has been regarded as the holotype. However, Lesueur referred to several specimens and did not mention a type in the original description; consequently I prefer to regard No. 8808 as a lectotype.

Lesueur also described *Trionyx ocellatus* (*op. cit.*:261-263) as a variety of *T. spiniferus* having ocelli, or parts thereof, on the carapace and mentioned three specimens. The total number of specimens that were available to Lesueur is unknown. One young alcoholic specimen having ocelli is in the British Museum (Natural History) (Gray, 1855:69). The same letter from Dr. Guibé stated that a specimen in the Museum of Natural History, Paris, No. 6957, having a carapace 17 centimeters in length, conforms to the characters of *ocellatus* as mentioned by Lesueur, and was obtained from the Wabash River by Lesueur. Two of the specimens mentioned by Lesueur (*loc. cit.*) are stated to be females. No. 6957 is an adult male and clearly shows the juvenal pattern; it is regarded as the lectotype of *T. ocellatus* Lesueur, a name-combination, which is a synonym, based on a secondary sexual difference in pattern.

Rafinesque (1832:64) described a soft-shelled turtle from "the River Hudson between the falls of Hadley, Glen and Baker, and further up to the source" as *Apalone hudsonica.* The most outstanding characteristic was the presence of five claws on the digits of each limb. Rafinesque's recording of this characteristic was perhaps influenced by the illustration of a softshell in Bartram's *Travels* that showed each limb with five, clawed digits. Perhaps this was the basis for Boulenger (1889:245, footnote) regarding *Apalone* as "mythical." The large, yellowish, black-bordered spots, one behind and one in front of the eye presumably represent segments of the postocular stripe and the stripe on the snout; Rafinesque described the carapace as "entire . . . the margin is yellowish unspotted, then comes a circular black line . . ." and having "many round spots occulated and clouded by having a brown margin, with grey dots within." Except for five claws, the description is applicable to a softshell and referable to *T. s. spinifer.* To my knowledge, the only other records of the occurrence of soft-shelled turtles in the Hudson river drainage are those of Eights (*in* Bishop, 1923:120, Mohawk River at Cohoes), and DeKay (1842:7, Mohawk River and Hudson River near Albany); presumably these records are the basis for the comments of Holbrook (*in* Bishop, *loc. cit.*), and symbolized as an isolated locality by Conant (1958:318, map 35). The type locality of *Apalone hudsonica* is herein restricted to the Hudson River, near Baker's Falls, Saratoga County, New York.

Gray (1844:48) proposed the name *Tyrse argus* for a specimen reported to have come from Sierra Leone, West Africa; later (1855:68) he referred the species to the genus *Trionyx.* After comparison with a specimen of *T. spiniferus* Lesueur, Gray (1864:89) was "doubtful whether there must not have been some confusion about the habitat of the specimen [which formed the basis of the description of *Tyrse argus*], and whether it is not more probably a North American species." The same author (1869:222; 1870:109) listed *Tyrse argus* as a synonym of *Callinia spinifera* (= *Trionyx spiniferus* Lesueur).

Agassiz (*op. cit.*:406-07) described *Aspidonectes nuchalis* on the basis of three adults from the Cumberland River and a number of young from the headwaters of the Tennessee River. Boulenger (1889:245, footnote 2) suggested that the status of *A. nuchalis* required further investigation. The species was not generally recognized after the turn of the century. Barbour and Loveridge (1929:226) listed MCZ 1908 (one of the juveniles) and 1623-25 as cotypes. Stejneger (1944:52) showed that *nuchalis* was not distinguishable from *T. s. spinifer*, and (*op. cit.*:49) listed MCZ 1623-25 as cotypes. Schmidt (1953:110) restricted the type locality to the Cumberland River, near Nashville, Tennessee.

Agassiz (*loc. cit.*) mentioned that *nuchalis* "differs strikingly from Asp. spinifer in the much more elongated form of the male, and in the great development of the marginal spines and of the tubercles upon the carapace, . . . But the most prominent specific character consists in the marked depressions on either side of the blunt median keel, and also in the triangular dilation of that keel behind the front margin of the carapace." These characters seem to be of no taxonomic worth. I have seen three syntypes (MCZ 1623-25) that undoubtedly correspond to the three adult specimens mentioned by Agassiz. All are females, measuring 19.5, 22.0, and 19.0 centimeters, respectively, in plastral length, and lack a contrasting mottled pattern on the carapace; the juvenal pattern is obscured, except for blackish spots at the edge of the carapace on MCZ 1625, and parts of an ocellus on MCZ 1624. The dorsal surfaces of the limbs are boldly marked. MCZ 1623, showing the diagnostic feature mentioned by Agassiz, is photographed by Stejneger (*op. cit.*:Pls. 14, 15), and may be regarded as the lectotype of *Aspidonectes nuchalis* Agassiz. MCZ 1908 is one of the young syntypes mentioned by Agassiz, and is referable to *spinifer*. The juvenal pattern consists of spots and ocelli; the plastron measures 3.1 centimeters in length, and the carapace 4.2 centimeters.

Wied-Neuwied (1865:55-57, Pl. 5) described the species ?*G [ymnopus] olivaceus*, but was uncertain whether his interpretation was based on a species, a variety or a secondary sexual difference. Wied-Neuwied mentioned that Lesueur had already named this soft-shelled turtle as *Trionyx ocellatus*, and agreed with Lesueur that those turtles having occulated spots on the carapace were distinguishable from *T. spiniferus* and *T. muticus*. But because Duméril and Bibron in their *Erpétologie Général* failed to recognize *T. ocellatus*, Wied-Neuwied felt obliged to bring it to the attention of his American colleagues and he renamed it. Wied-Neuwied also stated, in the context of a synonym, "Beschreibung einer Reise in Nord-America Bd. I., pag. 140." This comment presumably refers to his earlier description of *T. annulifer* (1838:140); seemingly Wied-Neuwied considered *T. annulifer* and *G. olivacea* as conspecific, although there is no mention of *annulifer* in the text proper. Stejneger (*op. cit.*:49) designated the type locality of *T. annulifer* as the Ohio River at Pittsburgh, Pennsylvania, and of *Gymnopus olivacea* as New Harmony, Wabash River, Illinois (*lapsus* for Indiana).

Trionyx spiniferus was questionably considered distinct from *T. ferox* by

Lesueur who listed "Testudo ferox Gm. Tortue de Pennant?" and "Trionyx georgicus Geoffr.?" as synonyms. Subsequently, most authors considered *T. spiniferus* synonymous with *T. ferox* until Agassiz (1857) pointed out differences between the two species.

The average size of the ocelli on the carapace of the subspecies *spinifer* decreases westward toward the Mississippi River; ocelli of different sizes occur on different individuals from the same state and presumably from the same population. For example, INHS 2281, plastron 9.9 centimeters in length, from Effingham County, Illinois, has some ocelli eight millimeters in diameter, whereas a larger male from the same locality, UI 1322, plastron 11.6 centimeters in length, has the largest ocelli only five millimeters in diameter. For convenience, all softshells having locality data from states east of the Mississippi River are referred to *spinifer*, recognizing that intergradation occurs with *hartwegi* over a broad area paralleling the Mississippi River. The type locality of *spinifer* is in an area where most turtles do not have the larger ocelli (diameter of seven to ten mm. on adult males); however, some individuals from the Wabash River (UMMZ 63523, adult male, plastron 11.5 cm. in length, ocelli diameter seven mm.) agree with more "typical" *spinifer* to the east. Intergradation with *asper* possibly occurs in that part of the Tennessee River in eastern Tennessee as exemplified by UMMZ 59198.

Published reports indicate that *T. s. spinifer* is not abundant in some of the northeasterly parts of its geographic range. Adams and Clark (1958:10) wrote that few softshells at Long Point on the Canadian side of Lake Erie are "ever collected and the area's game keepers report . . . (none) . . . seen in recent years. They also tell of recurrent severe stormy winters in which the muddy bottom of the marshland was repeatedly churned up and frozen. Such climatic conditions could easily destroy a large part of the *Trionyx* population overwintering in the mud bottom." Wright (1919:8) reported that softshells are "rarely seen" in bays on the New York side of Lake Ontario, and Babcock (1938:53) wrote that *spinifer* "is not common in Lake Champlain."

T. s. spinifer probably extended its geographic range into the Hudson River drainage of New York *via* the Erie Canal (connected Buffalo and Albany) after its completion in the early 1800's (DeKay, 1842:7). Now, the New York Barge Canal (essentially the Erie Canal, but with minor changes in course and the addition of several spurs) provides an avenue for dispersal of *spinifer* to the Hudson River drainage, Lake Ontario and intervening waterways in New York (Mertens, 1928:199). Netting (1944:86-87), however, suggested that *spinifer* occupied Lake Champlain, the Finger Lakes, Mohawk River and upper Hudson in the late stages of the formation of the Great Lakes.

A publication not seen by me is that of Mansueti and Wallace (1960). Its title suggests that *Trionyx* occurs in Maryland.

The unsuccessful introduction of *T. s. spinifer* in the Delaware drainage in New Jersey has been discussed by Fowler (1907:213), who wrote that they were found as early as the late 1860's and were introduced when young presumably to stock aquaria. Records of occurrence include Cooper's Creek, Camden County (Stone, 1906:168); Woodbury, Gloucester County (Cope, 1894:889); and Paulins Kill at Hainesburg, Warren County (Johnson, 1894:889).

Surface (1908:122) believed that soft-shelled turtles "have doubtless been introduced into the eastern part of Pennsylvania through the canal from the Western and Central part of New York," and Roddy (*in* Neill, 1951:21) suggested that the species may be found in the Susquehanna River. Babcock (1919:420) mentioned a young specimen of *spinifer* in the collection of the Boston Society of Natural History that was obtained "in White River, Vermont," a tributary of the Connecticut River of the Atlantic Coast drainage; seemingly this record has not been accepted and the species is not established. To my knowledge, populations of *T. s. spinifer* do not occur in rivers of the Atlantic Coast drainage, except probably the Hudson-Mohawk drainage.

Stockwell (1878:401) wrote that *spinifer* was found "as high as Athabasca." Presumably Stockwell referred to Lake Athabaska in northern Alberta and Saskatchewan, Canada, a region where soft-shelled turtles are unknown; see also the comments by Stejneger (1944:52).

Specimens examined.—Total 250 as follows: ALABAMA: *Morgan:* UMMZ 99578, "near" Decatur.

ILLINOIS: *Adams:* INHS 2150, Quincy. *Bond:* INHS 8345, Greenville. *Carroll:* CNHM 42116, Ordinance School Proving Ground. *Cass:* INHS 2151, Beardstown. *Champaign:* INHS 2273, 2311, 2413, 3142, "near" Seymour; INHS 4229, Champaign; INHS 6163, Sidney. *Christian:* INHS 1560, Pana. *Coles:* INHS 1968-69, 2 mi. W Charleston. *Cumberland:* INHS 2282, Greenup. *De Witt:* INHS 7674, Farmer City. *Effingham:* UI 1322, 2281, 19365, "near" Effingham. *Fulton:* INHS 5531, 2 mi. NE Bluff City, Schyler County; UI 23449, Liverpool; UI 24611, Spoon River, 18 mi. NW Canton. *Hancock:* USNM 53522, 59277, "near" Hamilton. *Iroquois:* INHS 6869-70, 2.5 mi. N Crescent City. *Jackson:* TU 1369 (12), Elkville. *Kane:* CNHM 42400, Aurora. *Kankakee:* CNHM 324, Momence. *Kendall:* UI 2411, Plano. *Logan:* INHS 7171-72, 6 mi. N Lincoln. *Madison:* USNM 60571. *Macoupin:* UI 2401-02, Beaver Dam Lake. *Mason:* CNHM 346, 470, INHS 1122, 1559, 5756-58, UI 42, 2404, Havana, Lake Chautauqua. *Mercer:* CNHM 3220, New Boston. *Morgan:* CNHM 2067 (2), 3290, 3303-04, 3306, INHS 2152, 2154, 5132-37, USNM 54747, Meredosia. *Moultrie:* INHS 8989, 2 mi. NW Lovington. *Peoria:* UI 2406-10, Peoria. *Pope:* INHS 5505, Lake Glendale. *Putnam:* UMMZ 81604-14, 5 mi. N Henry, Marshall County. *Schuyler:* UI 2405, "near" Ripley, Brown County. *Scott:* INHS 2149, 2153, Naples. *Union:* CNHM 18623, 6 mi. SW Jonesboro. *Vermilion:* INHS 3142, Muncie; INHS (1 untagged); UI 1970, 3209, Danville; UI 2403, 1.5 mi. E Oakwood; UI 16265, Kickapoo State Park. *Wabash:* USNM 12061, Mt. Carmel. *Winnebago:* INHS 7185, Kishwaukee Forest Preserve; INHS 7294, ½ mi. S Shirland. *County unknown:* USNM 7661.

INDIANA: *Bartholomew:* UMMZ 61060, 10 mi. W Columbus. *Carroll:* USNM 42905-06, Burlington. *Clark:* UMMZ 110599, 14-mile Creek, 3 mi. NW Charleston. *Decatur:* UMMZ 55416, 3 mi. S Westport. *Elkhart:* UMMZ 105598, Elkhart River, south of Goshen. *Gibson:* UMMZ 89744, Foot's Pond. *Johnson:* UMMZ 108062, 2 mi. S Trafalgar. *Knox:* USNM 22711, Vincennes. *Kosciusko:* AMNH 8379, UMNZ 84287 (5), Winona Lake; UMMZ 110235, Wawasee Lake. *Lake:* CNHM 11019, 11021-24, Crown Point. *Marion:* UMMZ 103393, Ravenswood; UMMZ 110236, 1 mi. N Lawrence. *Marshall:* CNHM 39299; USNM 33495, Yellow River north of Burr Oak; USNM 33496-501, 35404, 42583-84, Lake Maxinkuckee. *Wells:* UMMZ 63523, Wabash River, Bluffton. *County unknown* (Lagrange or Marshall): USNM 50670, Twin Lakes.

KENTUCKY: *Casey:* UMMZ 112252, trib. of Green River, south of Yosemite. *Green:* UMMZ 116718, Little Barren River, 1.5 mi. E Monroe, Hart County. *Rockcastle:* UMMZ 98767, Rockcastle River, 5 mi. above Livingston.

MICHIGAN: *Allegan:* UMMZ 42112, Kalamazoo River. *Barry:* UMMZ 53874, Thornapple River, 3 mi. NW Hastings. *Bay:* UMMZ 74670. *Branch:* UMMZ 95615, 1 mi. S Kinderhook; UMMZ 70748, Hog Creek. *Calhoun:* UMMZ 89950 (3); UMMZ 79133, near Battle Creek. *Cass:* UMMZ 40866-67, 53005, Diamond Lake; UMMZ 40868, 52948, Long Lake. *Jackson:* UMMZ

72494. *Kalamazoo:* UMMZ 42130, 80534, Kalamazoo; UMMZ 90506, Gull Lake; UMMZ 92599, Kellogg Bird Sanctuary. *Lenawee:* UMMZ 72457, Devil's Lake; UMMZ 74662, Wolf Lake Park. *Livingston:* UMMZ 54401, 76190, Portage Lake. *Monroe:* UMMZ 44604-06, USNM 51213, "near" Monroe. *Newaygo:* UMMZ 63469. *Oakland:* UMMZ 64363, Hay's Creek; UMMZ 96539, Clinton River. *Ottawa:* UMMZ 81699. *St. Joseph:* UMMZ 38876, 38889, "near" White Pigeon; UMMZ 96537, Corey Lake. *Van Buren:* UMMZ 90003, Wolf River, west of Kalamazoo, Kalamazoo County. *Washtenaw:* SM 2035, 2038, 2105, UMMZ 39847, 96538, "near" Ann Arbor; UMMZ 35765, 35769, 74518 (2), Portage Lake; UMMZ 54402-03, Little Lake; UMMZ 89659, Huron River, Dexter; UMMZ 110583-85. *County unknown* (Washtenaw or Livingston): UMMZ 54400, Huron River near Portage Lake.

MISSISSIPPI: *Adams:* MCZ 46615, UMMZ 76446, "near" Natchez; MCZ 46621, 46633, USNM 01084, 01086, Washington. *Coahoma:* AMNH 5289, 5285-86, Moon Lake. *Lafayette:* MCZ 37173, Oxford; USNM 7650, Abbeville? (reported from Abbeville, South Carolina by Pickens, 1927:113; see discussion by Stejneger, 1944:50, and my comments on page 509 beyond). *LeFlore:* USNM 73668-69, Greenwood. *Madison:* USNM 95192, Big Black River. *Washington:* USNM 115980, Deer Creek. *Yazoo:* UMMZ 86669, Panther Creek west of Yazoo City; UMMZ 83304, Yazoo City.

NEW YORK: *Monroe:* CNHM 92001-02, Genesee River, Rochester. *Wayne:* AMNH 69931, CNHM 92004, Sodus Bay.

OHIO: *Athens:* UMMZ 111793, east branch Shade Creek. *Franklin:* USNM 26290. *Lucas:* USNM 51214, Toledo. *Pike:* UMMZ 99309, Morgan's Fork, Sunfish Creek. *Warren:* AMNH 4763, Little Miami River, 3 mi. below Morrow. *County unknown:* USNM 21128-29, Cuyahoga River.

TENNESSEE: *Benton:* UMMZ 113036, Eagle Creek, ½ mi. E Holliday. *Bradley:* UMMZ 59197, west branch of Chestnee Creek, 7 mi. E Cleveland. *Claiborne:* USNM 86677, 5 mi. SE Cumberland Gap, Powell River. *Davidson:* MCZ 1623-25, Cumberland River near Nashville (restricted locality); USNM 7165-67, Nashville. *Decatur:* KU 3000, Perryville. *Hamilton:* USNM 131861, Chattanooga. *Monroe:* TU 16058, Little Tennessee River, 10 mi. N Madisonville. *Obion:* UMMZ 53199, USNM 102911, Reelfoot Lake. *Overton:* UMMZ 69561 (2), Wirmingham. *Sevier:* TU 16132, UMMZ 86735, USNM 86681-82, near Sevierville; UMMZ 86734, Walden Creek "near" Gatlinburg. *County unknown:* MCZ 1908, headwaters of Tennessee River.

VIRGINIA: *Smythe:* USNM 101386, Holston River, Seven Mile Ford.

WEST VIRGNIA: *McDowell:* USNM 33767, Dry Fork, Perryville (county questionable, perhaps Randolph County).

WISCONSIN: *Chippewa:* CNHM 8223, Lake Wissota, mouth of Yellow River, Anson Twp. *Polk:* UMMZ 72511-12, St. Croix River "near" Never's Dam. *County unknown:* CNHM 15971, Eau Claire River.

Records in the literature.—ONTARIO: *Carleton:* Ottawa (questionable record). *Essex:* Point Pelee. *Haldimand:* Dunville. *Kent:* Lake St. Clair. *Norfolk:* Long Point. *Oxford:* Beachville. *Wentworth:* Hamilton Bay (Logier and Toner, 1955:51).

QUEBEC: *Iberville:* Richelieu River at Iberville (Logier and Toner, 1955:51).

ALABAMA: *Lawrence:* Courtland (Stejneger, 1944:53).

ILLINOIS: *Boone:* Belvidere. *Bureau:* Bureau. *Cass:* Chandlerville. *Clay:* Louisville (Cahn, 1937:189). *Cook:* Lake Michigan (Kennicott *in* Stejneger, 1944:44); Evanston (Necker, 1939:10); Chicago (Schmidt and Necker, 1935:76). *Crawford:* Robinson. *Douglas:* northern part of county (P. W. Smith, 1947:39). *Fayette:* Vandalia. *Fulton:* Ellisville (Cahn, *loc. cit.*). *Grundy:* Morris (Stille and Edgren, 1948:201). *Jackson:* Jacob (Cagle, 1942:158). *Jersey:* Grafton (Cahn, *loc. cit.*). *Kane:* Batavia; Dundee Game Farm (Stille and Edgren, *loc. cit.*). *Kankakee:* Kankakee River near Altort (Necker, *loc. cit.*). *Lake:* Fox Lake. *LaSalle:* Streator (Cahn, *loc. cit.*). *Lawrence:* (Hahn *in* Stejneger, 1944:44). *Lee:* symbol on map (Cahn, *loc. cit.*). *McHenry:* McHenry (Stille and Edgren, *loc. cit.*). *Macon:* Decatur. *Macoupin:* Carlinville (Cahn, *loc. cit.*). *Ogle:* Oregon (Garman *in*

Cahn, *loc. cit.*). *Randolph:* Chester, Reily Lake. *Rock Island:* Barstow, Hillsdale, Rock Island (Cahn, *loc. cit.*). *Saline:* Horseshoe Lake (Stein, 1954: 312). *Stephenson:* Freeport (Cahn, *loc. cit.*). *Union:* Bluff Lake (Garman *in* Cahn, *loc. cit.*). *Whiteside:* Sterling, symbol on map (Cahn, *loc. cit.*). *Williamson:* Marion (Cagle, 1942:158). *Winnebago:* Rockton; symbol in western part of county (Cahn, *loc. cit.*). *County unknown:* Fox River (Yarrow, 1882:29).

INDIANA: *Brown:* 1 mi. below Helmsburg (Myers, 1927:339). *Clay:* Eel River (Kirsch *in* Stejneger, 1944:45). *Franklin:* (Hughes *in* Stejneger, *loc. cit.*). *Jasper:* Jasper-Pulaski Game Preserve (Swanson, 1939:690). *Jefferson:* Madison (Myers, *loc. cit.*). *Marion:* Irvington (Stejneger, *op. cit.*:55). *Marshall:* 2 mi. NW Culver (KKA). *Monroe:* Bloomington (McLain *in* Stejneger, *op. cit.*:45). *Newton:* Lake Village (Stille and Edgren, *loc. cit.*). *Posey:* Wabash River at New Harmony (Lesueur, 1827:257). *Starke:* Grant (Stille and Edgren, *loc. cit.*). *Steuben:* Fish Creek "near" Hamilton (Stejneger, *op. cit.*:53). *County unknown* (Knox or Starke): USNM 72387, Knox (Stejneger, *op. cit.*:55); "White Water valley," east-central part of state (Butler, 1894:224). USNM 8359 (= *Trionyx spinifer asper*) has been erroneously recorded from Madison, Indiana, by Yarrow (1882:29) and Hay (1892:145); see discussion by Cahn (1937:200) and Stejneger, (*op. cit.*:73, 75).

KENTUCKY: *Edmonson:* Green River, Mammoth Cave National Park (Hibbard, 1936:281). *Fleming:* Fox Creek (Welter and Carr, 1939:130). *Jefferson:* (Funkhouser, 1925:71). *Morgan:* (Stejneger, 1944:54). *County unknown:* Ohio and Pond rivers (Funkhouser, *loc. cit.*).

MICHIGAN: *Berrien:* mouth of St. Joseph River at St. Joseph (Lagler, 1943:303). *Eaton:* Brookfield; Olivet (Clark *in* Ruthven, Thompson and Thompson, 1912:133). *Genesee:* (Miles *in* Ruthven, Thompson and Thompson, *loc. cit.*). *Iosco:* (Lagler, 1943:283, symbol on map). *Kent:* (Lagler, *loc. cit.*). *Montcalm:* (Clark *in* Ruthven, Thompson and Thompson, *loc. cit.*). *Muskegon:* Muskegon River "near" Muskegon (Lagler, *op. cit.*:303). *Van Buren:* Reynolds Lake, 2.5 mi. E Lawrence (Edgren, 1942:180).

MISSISSIPPI: *De Soto:* Lake Cormorant (Stejneger, 1944:55). *Holmes:* Thornton (Cook, 1946:185). *Humphreys:* Belzoni (Stejneger, *loc. cit.*) *Sunflower: Warren:* Vicksburg, Eagle Lake (Cook, *loc. cit.*). *Washington:* Lake Washington (Smith and List, 1955:125); Greenville (Stejneger, *loc. cit.*).

NEW YORK: *Albany:* Hudson River at Albany (DeKay, 1842:7); Mohawk River at Cohoes (Eights *in* Bishop, 1923:120). *Cattaraugus:* Allegheny River and Red House Lake in Allegheny State Park (Eaton, 1945:115). *Chautauqua:* Lake Chautauqua (DeKay, *loc. cit.*). *Monroe:* Braddocks Bay and Long Pond on Lake Ontario (Wright, 1919:8). *Saratoga:* Hudson River near Baker's Falls (restricted locality, Rafinesque, 1832:64). *County unknown:* Lake Cayuga; Mohawk River (DeKay, *loc. cit.*).

OHIO (Conant, 1951:158-59, 264, except records from Allen, Geauga and Noble counties): *Allen:* Sugar Creek, 6 mi. N Lima (Adler and Dennis, 1960:27). *Ashland:* Long Lake, Lake Twp.; Black Fork, Sec. 27, Green Twp. *Athens:* Hocking River "near" Athens; "near" Fisher, Alexander Twp. *Auglaize:* Pushcta Creek, west of Wapakoneta. *Brown:* White Oak Creek, 1 mi. N Higginsport. *Butler:* Oxford. *Champaign:* Mad River, 4 mi. SW Urbana. *Coshocton:* Walhouding River, below dam. *Defiance:* Auglaize River, Shawnee Scout Camp, Defiance Twp. *Erie:* Huron; Sandusky. *Fairfield:* Buckeye Lake. *Franklin:* Alum Creek, Westerville; Columbus. *Geauga:* Chardon Twp. (Wood, 1959:8). *Greene:* Huffman Dam. *Hamilton:* Harrison; mouth of Miami River. *Hardin:* "near" Hepburn. *Henry:* Maumee River, east of Napoleon; Maumee River "near" Texas; Maumee River, 3 mi. W Texas. *Highland:* Little Brush Creek, 2 mi. N Sinking Spring. *Huron:* Huron River "near" Monroeville. *Jackson:* Canter's Cove, Jackson Twp.; Jackson Lake. *Knox:* Brinkhaven. *Lake:* east branch Chagrin River, Kirtland; Grand River, 4 mi. E Painesville. *Lawrence:* Pine Creek, Elizabeth Twp. *Logan:* Miami River, "near" Indian Lake. *Lorain:* Oberlin. *Lucas:* Lake Erie at Reno Beach, Jerusalem Twp.; Lake Erie, ½ mi. offshore from mouth of Crane Creek; Maumee River at Maumee; Swan Creek, W of Toledo; "near" Waterville; Swan Creek "near" Whitehorse. *Madison:* London. *Me-*

dina: Hinckley Lake. *Meigs:* Shade River, below Darwin. *Miami:* Miami River, above Troy. *Monroe:* Cranenest Fork, Green Twp. *Montgomery:* Mad River, Dayton; Miami River, Dayton; Stillwater River, Dayton. *Morrow:* Kokosing River, Franklin Twp. *Noble:* Jct. Sharon Twp. 1 and St. Rt. 78. (Adler and Dennis, 1960:27). *Ottawa:* East Harbour, Catawba Island. *Pike:* Chenoweth Fork, Sunfish Twp.; Scioto River, Camp Creek Twp. *Ross:* Paint Creek near Bainbridge. *Vinton:* Lake Hope; Lake Alma. *Warren:* Fort Ancient. *Washington:* Dam No. 2, Muskingum River, "near" Marietta. *Williams:* 1 mi. S Blakesley; St. Joseph River "near" Blakesley; West Branch, St. Joseph River, Sec. 8, Bridgewater Twp.; Edgerton. *Wood:* Grand Rapids; Grassy Creek, Rossford; Haskins; Maumee River opposite Toledo.

PENNSYLVANIA: *Allegheny:* Monongahela River above McKeesport (Atkinson, 1901:154); Ohio River at Pittsburgh (Wied-Neuwied *in* Stejneger, 1944: 44, 49). *Armstrong:* (Swanson, 1952:165). *Clarion:* Clarion River "near" Clarion (Allen, 1955:228); Foxburg (=Foxbury?, Boulenger, 1889:260). *Crawford: Elk: Erie:* Edinboro Lake. *Forest:* (Swanson, *loc. cit.*). *Indiana:* Plum Creek; Crooked Creek (Netting *in* Stejneger, 1944:48). *McKean:* (Swanson, *loc. cit.*). *Somerset:* Stoyestown (Surface, 1908:122). *Warren: Venango:* Allegheny River south of Franklin (Swanson, *loc. cit.*).

TENNESSEE: *Chester:* South Fork, Forked Deer River just E Henderson (Endsley 1954:40). *Clay:* Mill Creek, 3 mi. from Butler's Landing; Obey River above mouth of Wolf River at Lilydale; mouth of Wolf River (Shoup, Peyton and Gentry, 1941:75); Iron Creek "near" Willow Grove (Stejneger, 1944:56). *Fentress: Jackson:* (Gentry, 1941:332). *Lake:* Reelfoot Lake (Parker, 1948:29). *Obion:* Walnut Log (Parker, 1937:85); east shore of Reelfoot Lake, Samburg (Rhoads, 1895:386). *Overton:* Medlock Branch, tributary of West Fork Obey River north of Allred (Shoup, Peyton and Gentry, *loc. cit.*). *Roane:* 2 mi. S Kingston (Stejneger, 1944:55).

VERMONT: *Chittenden:* Lake Champlain, mouth of Winooski River; "near" Burlington; Milton (=Minton) (Babcock, 1919:420). *Franklin:* Swanton (Stejneger, 1944:55).

WEST VIRGINIA: *Randolph:* Tygart River at Elkins (Green, 1937:116).

WISCONSIN: *Burnett: Crawford:* (Pope and Dickinson, 1928:83). *Dane:* Lake Wingra, Madison (Noland, 1951:54). *Grant:* (Pope and Dickinson, *loc. cit.*). *Green Lake:* Berlin (AMNH 6840-41, listed in card file March 2, 1959). *Jefferson:* Lake Mills (Dickinson, 1950:75). *La Crosse:* West Salem (Pope, 1930:281). *Oneida: Pepin:* (Pope and Dickinson, *loc. cit.*). *Racine:* Eagle Lake (Edgren, 1944:498); Burlington; Rochester (Stille and Edgren, 1948: 201). *Sheboygan:* Sheboygan (KKA). *Trempealeau: Vernon:* "near" Viroqua (Pope, *loc. cit.*). *Walworth:* Lake Beulah (Dickinson, *loc. cit.*). *Washburn:* (Pope and Dickinson, *loc. cit.*). *Waukesha:* Lac La Belle (Cahn, 1929:8). *Winnebago:* Wolfe River (Dickinson, *loc. cit.*).

Trionyx spinifer hartwegi (Conant and Goin)

Western Spiny Softshell

Plates 35 and 36

Amyda spinifera hartwegi Conant and Goin, Occas, Papers Mus. Zool. Univ. Mich., No. 510:1, pl. 1, map 1, June 15, 1948.

T[rionyx] s[pinifer] hartwegi Schwartz, Charleston Mus. Leaflet, No. 26:11, May, 1956.

Type.—Holotype, UMMZ 95365; alcoholic adult male; obtained at Wichita, Sedgwick County, Kansas, in May, 1945, by Robert Young.

Range.—Central United States in tributaries flowing into the Mississippi River from the west, except the Red River drainage; eastern Montana, North Dakota, and southern Minnesota south to eastern Colorado, northern Oklahoma and Arkansas (see map, Fig. 19).

Diagnosis.—Juvenal pattern of small ocelli, rarely as large as two millimeters in diameter, or usually solid black dots that are not much larger in center of carapace than at sides (mean OD/PL, Kansas, .022); only one dark marginal line separating pale rim of carapace from dorsal ground color.

Description.—Plastral length of smallest hatchling, 2.8 centimeters (USNM 9928); of largest male, 13.1 centimeters (USNM 55687); of largest female, 25.5 centimeters (KU 2283).

Carapace olive, having small ocelli or black spots that are not much larger in the center of the carapace than at the sides; pale rim of carapace separated from darker ground color by one dark marginal line and not four or five times wider posteriorly than laterally; large females often having black dots at sides of carapace on mottled and blotched pattern; pattern on snout of pale, dark-bordered stripes that unite forming acute angle in front of eyes; well-defined dark markings in subocular and postlabial region; pattern contrasting with ground color on side of head; postlabial stripe broken, interrupted; pale postocular stripe having blackish borders interrupted, not joining with postlabial stripes; dorsal surface of soft parts of body having contrasting pattern, largest blackish marks on hind limbs; elongate tail of males having pale dorsolateral bands with well-defined, lower, blackish borders; patterns on soft parts of body usually obscured or absent on large females; underparts whitish, often having blackish marks, except in center of plastral area; dark marks on webbing of limbs, palms and soles; dark streaks often coincident with digits; tubercles along anterior edge of carapace small and conical on adult males, and conical or knoblike on large females; accessory, knoblike tubercles in nuchal region and in middle of carapace posteriorly on large females.

Ontogenetic variation in PL/HW, mean PL/HW of specimens having plastral lengths 7.0 centimeters or less, 4.24, and exceeding 7.0 centimeters, 5.33; ontogenetic variation in CL/CW, mean CL/CW of specimens having plastral lengths 8.5 centimeters or less, 1.12, and exceeding 8.5 centimeters, 1.19; mean CL/PCW, 2.00; mean SL/HW, 1.30 (including subspecies *spinifer*); mean CL/PL, 1.38.

Variation.—Variants include: CNHM 8949, UMMZ 72511 and TU 14591 having ocelli approximately 4 millimeters in diameter that are almost solid spots; KU 17728 having pale stripes on snout that lack black, inner borders; TTC 719 (female, plastral length 20.7 cm.), having distinct pattern on snout; USNM 14535, 17823, 55684, and 123446 (from different localities) having markings confined to margins of carapace (Stejneger, 1944:66, suggested that USNM 17823 probably came from Texas); UMMZ 92667 (female, plastral length 6.7 cm.) lacking pattern on carapace.

Comparisons.—*T. s. hartwegi* can be distinguished from all other subspecies of *T. spinifer* by the presence of small dots and ocelli on the carapace that are all of approximately the same size in combination with only one dark marginal line. *T. s. hartwegi* resembles *asper* in having small blackish ocelli or dots on the carapace but differs from *asper* in having only one dark marginal line. *T. s. hartwegi* differs from *spinifer* only in the small size of the ocelli. *T. s. hartwegi* resembles *spinifer* and *asper*, but differs from *pallidus, guadalupensis* and *emoryi* in having blackish spots and ocelli on the carapace and lacking small whitish spots. *T. s. hartwegi* resembles *spinifer, asper* and *pallidus* but differs from *guadalupensis* and *emoryi* in having conical or knoblike tubercles on the anterior edge of the carapace on large females.

T. s. hartwegi differs from the subspecies *asper, guadalupensis* and *emoryi* in having a narrower head, and from *emoryi* in having a wider carapace. *T. s. hartwegi* resembles *spinifer* and *asper* but differs from the other subspecies in having the carapace widest at a plane approximately one-half way back on the carapace. *T. s. hartwegi* and *spinifer* have longer snouts than do *pallidus* and *guadalupensis* or *emoryi*. *T. s. hartwegi* differs from *asper* but resembles the other subspecies in having a relatively longer plastron.

Remarks.—The validity of *T. s. hartwegi* has never been questioned. It intergrades with *spinifer* over a broad area paralleling the Mississippi River. For convenience, specimens occurring west of the Mississippi River are referred to the subspecies *hartwegi*. Figure 8 shows much variation in size of ocelli on different individuals from the same state. For example, UMMZ 92667, plastral length 6.7 centimeters has a uniform pale brown carapace lacking any dark marks, whereas UMMZ 92652, plastral length 5.9 centimeters has some ocelli three millimeters in diameter on the carapace. Both are from Iowa. One specimen from Kansas, KU 1954 (Doniphan County, plastral length 11.8 cm.), has ocelli four millimeters in diameter, and USNM 7648 captured farther west at Fort Laramie, Wyoming, an adult male having a plastral length of 11.0 centimeters, has some ocelli five millimeters in diameter on the carapace. TTC 1090, an adult male from the panhandle of Texas has some ocelli so much as 5.5 millimeters in diameter. The size of the ocelli seemingly varies in the same local population.

Specimens of *T. spinifer* in the lower Mississippi Valley are intergrades. Most individuals have small black dots on the carapace; some have small ocelli (TU 7216, 7501, 11912, 12123-24) interspersed with black dots (TU 5863), others have black dots confined to the edge of the carapace (TU 157, 4539, 7105), and still others have no pattern on the carapace (TU 7506, 13698.1, 10087.6). Two large males (TU 11580, 13025) have large ocelli (approximately five mm. in diameter) that have nearly black centers. In general, there is more dark pigmentation than farther north; some specimens have extensive pigmentation on the ventral surface of the carapace and soft parts of the body (TU 156, 5648). The dorsal surface of the limbs, especially the hind limbs, have a bold, black marbling and may be almost completely black (TU 5484, 5597). Many females, not exceeding plastral lengths of 7.0 centimeters, have a pale blotched pattern of lichenlike figures or have ill-defined black dots on the carapace (TU 10087, 13698.13, 13753.15).

Localities of specimens of *T. spinifer* occuring in the Mississippi River drainage in Mississippi are arbitrarily listed under the account of the subspecies *spinifer*, whereas those in Louisiana (excluding *pallidus*) are listed under the account of *hartwegi*.

Neither Over (1943) nor Wheeler (1947:169) record *T. s. hartwegi*, respectively, from South Dakota or North Dakota; records from the Missouri River drainage in Montana suggest the occurrence of the species in that drainage in North and South Dakota.

Specimens examined.—Total, 392 as follows: ARKANSAS: *Clay:* UMMZ 70735 (2), 7 mi. S St. Francis. *Crawford:* USNM 95352, Lee Creek, 7 mi. NW Natural Dam. *Drew:* CNHM 40785. *Lafayette:* KU 2225-29, 2944 (one of three specimens bearing last catalog number), 2963 (one of three specimens bearing this catalog number), 2964 (one of two specimens bearing this catalog number), Lewisville (see remarks under the account of the subspecies *pallidus*). *Lawrence:* CNHM 8949; CNHM 12598-600, 12602-04, TU 5855, UI 2413, Imboden; UI 2412, Black River at Powhatan. *Marion:* TU 14591 (6), White River at Cotter. *Prairie:* KU 1867, 1869, 1879, 1949-51, 2280-83, 2285-91 (2 specimens bear catalog number 2287), 2307, 2761-62, 2666, 2826, 2842, 3346-47, White River at DeValls Bluff. *Pulaski:* UMMZ 96540, Little Rock. *Saline:* USNM 17823, Saline River at Benton. *Searcy:* UMMZ 92755, Little Red River, 1.5 mi. SE Leslie. *Yell:* TU 14565, Petit Jean Creek, 10 mi. N Casa. *County unknown:* CNHM 28566-67, Ouachita River.

Iowa: *Allamakee:* UMMZ 72556-58, 92642-49, Mississippi River "near" Lansing. *Appanoose:* UMMZ 92667, Chariton River, 4.3 mi. N. Centerville. *Decatur:* UMMZ 92651, Grand River, 3.5 mi. WSW Decatur. *Dickinson:* UMMZ 55249, Milford; UMMZ 92655, Spirit Lake Twp. *Hamilton:* USNM 9928, Webster City. *Hardin:* UMMZ 92650, Eldora. *Louisa:* UMMZ 92654, Muscatine Slough, 12 mi. SW Muscatine, Muscatine County. *Muscatine:* INHS 7675, 5.5 mi. SE Muscatine; USNM 54730-32, Fairport. *Scott:* CNHM 433, Davenport; UMMZ 92656, Steamboat Slough, 2 mi. N Princeton. *Story:* UMMZ 92653, Squaw Creek at Ames. *Washington:* UMMZ 92652, English River, 2 mi. E Riverside.

Kansas: *Anderson:* KU 52286-87, 3¼ mi. E, ½ mi. N Colony. *Atchison:* UMMZ 66939-41, Atchison. *Barber:* KU 17728, 4.5 mi. S Sun City; KU 41379, 41742, 6 mi. N, 3.5 mi. E Sharon; USNM 100580, Medicine River, 1 mi. S Lake City. *Cherokee:* KU 1323, Galena. *Comanche:* KU 18385, 3-4 mi. SE Arrington. *Cowley:* UMMZ 75963, USNM 90441-44, 91022, 100529-30, "near" Winfield. *Doniphan:* KU 1943, 1952-54, Doniphan Lake. *Douglas:* KU 1955-56, Wakarusa River; KU 40176-77, Kansas River at Lawrence. *Franklin:* KU 3290. *Hamilton:* KU 2990, Syracuse. *Harper:* KU 18159 1 mi. N Harper. *Kingman:* USNM 95261, 2 mi. E Calista. *Labette:* KU 3339. *Lane:* KU 3738-41, Pendennis. *Logan:* KU 16531, Smoky Hill River, 3 mi. SW Elkader. *Meade:* KU 40210, Crooked Creek, 12.5 mi. S, 1¼ mi. W Meade. *Montgomery:* KU 3731-32, Independence; KU 50856, Cherryvale Lake. *Neosho:* UMMZ 69294, Caneville Creek, 32 mi. N. Parsons, Labette County. *Osage:* KU 3294-96, Appanoose Creek. *Pratt:* KU 15931-32, 15934, State Fish Hatchery "near" Pratt. *Riley:* KU 48239, McDowell Creek, WSW Manhattan; UMMZ 64434, "near" Manhattan. *Russell:* KU 3289. *Sedgwick:* UMMZ 95363-65, Wichita. *Shawnee:* USNM 123446, Kansas River at Topeka. *Stafford:* KU 3758, Little Salt Marsh; KU 41743, 13.5 mi. N, 6 mi. E Stafford. *Trego:* KU 2757, 3769, Smoky Hill River, 10 mi. N (NNE) Utica, Ness County; KU 51517, Saline River, 5 mi. N, ½ mi. E Wakeeney. *Wilson:* KU 56744-45, Verdigris River, 1 mi. S Altoona. *Woodson:* KU 55295, Neosho River, ½ mi. E, 1½ mi. S Neosho Falls. *County unknown:* USNM 51529.

Louisiana: *Catahoula:* TU 12629, Ouachita River, 4 mi. N Harrisonburg. *Claiborne:* TU 13080, Caney Lake "near" Summerfield. *Concordia:* KU 50849, Tensas River at Clayton; TU 16524 (3), USNM 012349, Lake Concordia; USNM 99865, Red River "near" Shaw. *East Carrol:* TU 827-30, 905, 5644-45, Lake Providence. *Grant:* TU 12735, Big Creek at Fishville, "near" Pollock. *Jefferson:* TU 5592-98, 7184, 10741, 10171, Mahogany Pond. *Lafourche:* TU 7105, 7132, 7216, 7501, 7505-07, 10087 (14), 11828-29, 11912, 11983 (2), 12123-28, 13502, 13679 (8), 13753 (22), 13766.2, Bayou Lafourche at Raceland. *Morehouse:* USNM 11631 (2), Mer Rouge. *Natchitoches:* USNM 100420, Cane River "near" Natchitoches. *Orleans:* TU 16169 (3), Audubon Park, New Orleans; USNM 029310, "near" New Orleans. *Ouachita:* TU 12916, 12954, 12970-71, 13019, 13025, Bartholomew Bayou at Sterlington; TU 5988, Monroe. *Pointe Coupee:* TU 153, 156-59, 165, 5484, 5513, 5518-19, 5646, 5648, 5651, USNM 100202-12, False River at New Roads. *Rapides:* TU 14040, Red River at Rapides. *Richland:* OU 25082. *St. Bernard:* TU 16170, Delacroix Island. *St. Charles:* TU 4539, 4579, 5224, 5990, 11928 (12), 13698 (16), Bayou Gauche between Paradis and Des Allemands; TU 5863, 11580, Bonnet Carre Spillway at Norco. *Tensas:* TU 5762, Lake St. Joseph near Newellton. *Union:* USNM 138946, Meridian Creek, 1 mi. E Conway; USNM 138947, Ouachita River, Alabama Landing. *Parish unknown:* MCZ 1622, Lake St. John (Concordia or Tensas Parish); USNM 029266, Louisiana?

MINNESOTA: *Hennepin:* AMNH 4759-60, Fort Snelling. *Lesueur:* KU 46742-43, Waterville, Lake Tetonka. *Winona:* USNM 59263-66, Homer.

MISSOURI: *Carter:* UMMZ 70737, "near" Van Buren. *Chariton:* UI 17509, Triplett. *Franklin:* USNM 55689. *Gasconade:* UMMZ 95900, Bourbeuse Creek, 8 mi. S Owensville. *Jefferson:* USNM 95405, Glaize Creek. *Lewis:* USNM 59279-80, Canton. *Miller:* UMMZ 91929, Barren Fork Tavern Creek, 5 mi. NW Iowna. *Newton:* UMMZ 82822, Shoal Creek, 12 mi. W Momit. *Phelps:* UMMZ 91930, Bourbeuse River, 10 mi. N St. James. *Reynolds:* CNHM 35392, Black River at Warner Bay Spring; USNM 55688. *Ripley:* UMMZ 90435. *Shannon:* INHS 6223, Alley Spring State Park. *St. Charles:* USNM 93089-94, Dardenne Creek, St. Peters. *St. Louis:* USNM 55685-87, Mississippi River at St. Louis. *Stone:* USNM 55684. *Washington:* USNM 55690. *Wayne:* UI 16554, Sam A. Baker State Park; UMMZ 95879, St. Francis River at Lodi. *County unknown* (Wayne or Butler): UMMZ 83264, Clark National Forest, St. Francis River.

MONTANA: *Big Horn:* USNM 54421, Crow Agency. *Roosevelt:* USNM 58, Fort Union (locality reads "Yellowstone, Fort Union"; probably the Yellowstone River near Fort Union). *Wheatland:* UMMZ 92005, Musselshell River near Shawmut. *Yellowstone:* USNM 14535, Custer.

OKLAHOMA: *Alfalfa:* OU 9316, 2 mi. S Cherokee. *Cleveland:* OU 22973, Norman. *Delaware:* UMMZ 81476, Spavinaw. *LeFlore:* OU 16802, 1.5 mi. E Zoe. *Osage:* UMMZ 89628, Big Hominy Creek. *Pottawatomie:* OU 25175, 5 mi. SW Shawnee. *Rogers:* OU 7317, Verdigris River, 5 mi. W Claremore; UMMZ 81473-74, near Garnett, Tulsa County; UMMZ 81475, 4 mi. NE Inola. *Sequoyah:* OU 9008, 2 mi. NE Gore; TU 13885, Little Vian Creek, 1 mi. E Vian. *Texas:* OU 5005, 5 mi. SE Guymon. *Tulsa:* TU 17061, Bird Creek "near" Skiatook, Osage County. *Woods:* CHNM 11809, Waynoka; OU 9432, 2.5 mi. W Waynoka; OU 9579, 9581-82, 1 mi. S Waynoka.

TEXAS: *Hansford:* TTC 719, 10 mi. S, 2 mi. W Gruver. *Hutchinson:* TTC 1090, Carson Creek, Turkey Track Ranch.

WYOMING: *Goshen:* USNM 7648, Fort Laramie. *Weston:* UMMZ 78080, Beaver Creek.

NO DATA: CNHM 21687-88, 22925. SM 142 (locality of Waco, McLennan County, Texas, believed in error). USNM 7649, 11625, 19622-23, 36412 (Illinois River).

Records in the literature.—ARKANSAS: *Benton:* (Dowling, 1957:37). *Chicot:* Lake Chicot. *Clark:* Terre Noir Creek, 13 mi. W Arkadelphia. *Garland:* Ouachita River, Mountain Pine (Conant and Goin, 1948:7). *Hempstead: Jefferson:* (Dowling, *loc. cit.*). *Lawrence:* Black Rock (Dellinger and Black, 1938:46). *Madison: Scott: St. Francis:* (Dowling, *loc. cit.*). *Washington:* near Greenland (Dellinger and Black, *loc. cit.*).

COLORADO: *Boulder:* Boulder Creek, E Boulder; Boulder Creek, 6 mi. S and 1 mi. E Longmont. *Larimer:* Cache la Poudre River. *Logan:* 8 mi. NE Sterling. *Morgan:* Platte River "near" Fort Morgan. *Otero:* Purgatoire River at Higbee. *Prowers:* Arkansas River at Lamar. *Weld:* Poudre River "near" Greeley; Evans. *Yuma:* Bonny Dam, Republican River (Maslin, 1959:24-25).

IOWA: *Dickinson:* Little Sioux River, Okoboji Twp. (Blanchard, 1923:24). *Story:* Skunk River, 5 mi. NNE Ames (Conant and Goin, 1948:9).

KANSAS: *Allen:* Petrolia (KKA). *Barber:* 7 mi. S Sun City. *Butler:* 3 mi. SE Augusta (Burt and Hoyle, 1934:198). *Chase:* 10 mi. SW Olpe; 7 mi. SW Saffordville (Breukelman and Smith, 1946:112). *Cherokee:* tributary of Spring River, 1 mi. N Riverton (Hall and Smith, 1947:451). *Coffey:* (Smith, 1956:160, symbol on map). *Cowley:* 11 mi. SE Winfield (Stejneger, 1944:55). *Crawford:* Pittsburg (Hall and Smith, *loc. cit.*). *Doniphan:* "near" Geary (Linsdale, 1927:81). *Elk:* (Smith, *loc. cit.*). *Ellis:* Big Creek (Brennan, 1934:190); Ellis (Conant and Goin, 1948:2). *Franklin:* Middle Creek, SE part of county (Gloyd, 1928:135). *Greenwood:* (Stejneger, *op. cit.*:54). *Leavenworth:* Missouri River "near" Fort Leavenworth (Brumwell, 1951:208). *Lyon:* 5 mi. E Emporia (Breukelman and Smith, *loc. cit.*). *Marion:* (Smith, *loc. cit.*). *Meade:* Meade County State Park, *ca.* 13 mi. SW Meade (Tihen and Sprague, 1939:505). *Ness:* 5.5 mi. NW Ness (Breukelman and Smith, *loc. cit.*). *Osage:* Marais des Cygnes River; Long and Jordan Creeks (Clarke, 1958:21). *Reno:* 6 mi. E Turon. *Sedgwick:* 2 mi. NE Cheney (Burt, 1935: 321). *Sheridan:* State Lake 7 mi. NE Quinter, Gove County (Breukelman and Smith, *loc. cit.*). *Wabaunsee:* Dragoon Creek at Harveyville (Clarke, 1956:215). *Wallace:* (Burt, 1933:208). *Wilson:* Fall River, ½ mi. S Neodesha (Clarke, *loc. cit.*).

MINNESOTA: *Anoka: Benton: Chisago:* (Breckenridge, 1944:184, symbols on map). *Crow Wing:* (Breckenridge, *op. cit.*:185). *Dakota:* (Hedrick and Holmes, 1956:126). *Goodhue:* (Breckenridge, *op. cit.*:184, symbol on map). *Hennepin:* Minneapolis; Lake Minnetonka (Breckenridge, *op. cit.*:187); 5 mi. N. Minneapolis (Breckenridge, 1955:5). *Houston:* Root River near Hokah. *Lesueur:* Lake Washington (Hedrick and Holmes, *loc. cit.*). *Meeker:* Swan Lake (Breckenridge, 1957:232). *Pine:* (Breckenridge, 1944:185). *Ramsey: Rice: Sherburne: Stearns:* (Breckenridge, *op. cit.*:184, symbols on map). *Washington:* just north of Stillwater (Hedrick and Holmes, *loc. cit.*). *Winona:* Winona (Breckenridge, *op. cit.*:187). *Yellow Medicine:* (Breckenridge, *op. cit.*:185). *County unknown* (Goodhue or Wabasha): Lake Pepin (Breckenridge, *op. cit.*:184)..

MISSOURI: *Boone:* east of Ashland (Henning, 1938:92). *Jackson:* Missouri River "near" Atherton (Anderson, 1942:219). *Jefferson:* Mississippi River "near" mouth Glaize Creek at Sulphur Springs; Glaize Creek at Barnhart (Boyer and Heinze, 1934:199). *St. Clair:* Osage River "near" Osceola. *Vernon:* Marmaton River, 7 mi. N Moundville (Conant and Goin, 1948:9).

MONTANA: Yellowstone River (Conant and Goin, 1948:9).

NEBRASKA: *Adams:* 1 mi. N Ayr (Hudson, 1942:101). *Dawson:* 2 mi. SE Gothenburg (Gehlbach and Collette, 1959:142). *Franklin:* 2 mi. SW Naponee. *Gage:* 1 mi. W Barnston. *Hitchcock:* 3 mi. E Stratton. *Holt:* Elkhorn River "near" Atkinson. *Lancaster:* Lincoln (Hudson, *loc. cit.*). *Lincoln:* 1 mi. S Sutherland (Gehlbach and Collette, *loc. cit.*). *Red Willow:* 14 mi. NW McCook. *Richardson:* 2 mi. S Rulo. *Wheeler:* 2 mi. W Ericson (Hudson, *loc. cit.*).

OKLAHOMA: *LeFlore:* Wister (Conant and Goin, 1948:9); Shady Pointe (KKA); Poteau River, 6.5 mi. W Heavener (Trowbridge, 1937:301). *Tulsa:* Arkansas River "near" Tulsa (Force, 1930:38).

WYOMING: *Goshen:* Platte River (Conant and Goin, 1948:10).

Trionyx spinifer asper (Agassiz)

Gulf Coast Spiny Softshell

Plates 37 and 38

Aspidonectes asper Agassiz, Contr. Nat. Hist. United States, 1(Pt. 2):405; 2(Pt. 3):pl. 6, fig. 3, 1857.

Trionyx spinifer asper Schwartz, Charleston Mus. Leaflet, No. 26:17, pls. 1-3, map 2, May, 1956.

Platypeltis agassizii Baur, Amer. Nat., 22:1121, 1888.

Type.—Lectotype, MCZ 1597; alcoholic female; locality designated as Pearl River, Columbus, Marion County, Mississippi; received from Mr. Winthrop Sargent of Natchez, Mississippi.

Range.—Southeastern United States except peninsular Florida from the Florida Parishes of Louisiana east to southern North Carolina; Gulf Coast drainage including that of Lake Pontchartrain, Louisiana, eastward to the Apalachicola River system, and Atlantic Coast drainage including that of the Altamaha River in Georgia northward to the Pee Dee River drainage in South Carolina (see map, Fig 19).

Diagnosis.—Juvenal pattern of black ocelli and spots, and two or more black, interrupted, lines paralleling rear margin of carapace; pale postocular and postlabial stripes often united on side of head; length of plastron short.

Description.—Plastral length of smallest hatchling, 2.9 centimeters (USNM 134244); of largest male, 13.2 centimeters (TU 17117); of largest female, 27.0 centimeters (TU 13474).

Blackish marginal rings on carapace number two, three or four posteriorly, but decrease in number anteriorly; segments of marginal rings may extend to nuchal region; marginal rings increasingly interrupted inwardly; pattern of hatchlings having well-defined marginal rings that are not extensively interrupted (often males), or having marginal rings broken into small segments or series of dots, and pale outer margin of carapace marked by ill-defined, hazy, inner border (often females); conspicuous marginal rings often lacking on hatchling females; pale rim of carapace not four or five times wider posteriorly than laterally; carapace having blackish dots, spots, small ocelli or a combination thereof; marks on carapace of slightly varying sizes, some occasionally barlike (usually males); some hatchling females showing pale, irregular blotching on carapace, often characterized by small lichenlike figures superimposed on blackish dots.

Striping on snout variable; pale, dark-bordered stripes usually unite in front of eyes and form right or acute angle; medial dark borders of pale stripes on snout not joined anteriorly, broken into segments or dots, reduced to single median line, united to form straight line connecting anterior margins of orbits (usually with slight medial indentation), or absent; pale postocular and postlabial stripes often joined, relationship variable and on either side of head; side of head with or without dark markings, sometimes a pale subocular blotch bordered below by a dark line; pattern on dorsal portions of soft parts of body contrasting, less so on limbs of hatchlings; pattern of irregular dark marks, dark streaks usually coincident with digits; longitudinal streaks often occur on neck; elongate tail of adult males usually having well-defined, dorsolateral, pale bands with dark lower border more diffuse than upper border.

Underparts whitish often with dusky markings on rear of carapace or in region of bridge; blackish marks often on webbing and portions of soles and palms, and chin and throat.

Small conical tubercles along anterior edge of carapace on adult males; remnants of juvenal pattern usually present on carapace of large females; conical or knoblike tubercles on anterior edge of carapace of large females; accessory knoblike tubercles in nuchal region (a paravertebral pair usually most prominent), and posteriorly in middle of carapace on large females.

Ontogenetic variation in PL/HW, mean PL/HW of specimens having plastral lengths 7.0 centimeters or less, 3.87, and exceeding 7.0 centimeters, 4.94; ontogenetic variation in CL/CW, mean CL/CW of specimens having plastral lengths 8.5 centimeters or less, 1.11, and exceeding 8.5 centimeters, 1.16; mean CL/PCW, 1.71; mean CL/PL, 1.45.

Variation.—The sex of some hatchlings can be distinguished by the pattern on the carapace (see Plate 37 for different patterns), but the sex of many hatchlings cannot be distinguished on the basis of pattern.

In the early stages of this study, I thought that the pattern on the carapace differed in eastern and western populations, and that the zone of intergradation was in Alabama. Adult males from the Tombigbee-Alabama river drainage and westward were noted to have blackish spots (some slightly ocellate) intermixed with few, if any, smaller blackish dots, whereas the adult males from east of the Tombigbee-Alabama river drainage had many small, black dots intermixed with slightly larger, mostly ocellate marks (see Plate 38, left, top and bottom, for contrast); also, hatchlings from western populations were never observed to have four marginal rings. On the basis of pattern, I would have thought that the individual having many ocelli, that lacks correct locality data and that is photographed by Stejneger (1944:Pl. 26), came from Georgia or South Carolina; but, the pattern (*op. cit.*:Pl. 27) of a specimen, probably an adult male, from South Carolina, resembles the pattern on adult males from Louisiana. The differences noted above are probably due to individual variation rather than geographic variation.

Color notes taken from life of a freshly-killed adult male (TU 16071, Louisiana) are: carapace olive, spots blackish, outer rim buff; top of head olive, postocular and postlabial stripes yellow with blackish borders, stripes on snout buff with blackish borders; dorsal ground color of soft parts of body pale olive-green, larger marks blackish, ground color laterally toward juncture of pattern and immaculate undersurface, and toward insertions of neck and limbs becoming yellowish; webbing on hind limbs having reddish tinge; dorsolateral bands on tail yellow with blackish borders; undersurface whitish; chin and throat olive-green with blackish marks; becoming buff then whitish posteriorly.

Occasional specimens have only one definite dark line paralleling the rear margin of the carapace. Schwartz (1956:16) reported that Charleston Museum No. 55.159.26 has only one solid line at the margin of the carapace, and I received an adult male (KU 47120) reported to have come from the Pearl River that is aberrant in not having more than one dark marginal line. USNM 95191, a large stuffed female from the Pearl River is mentioned by Stejneger (1944:59, Pl. 17) as having marks that "assume the form of short lines parallel

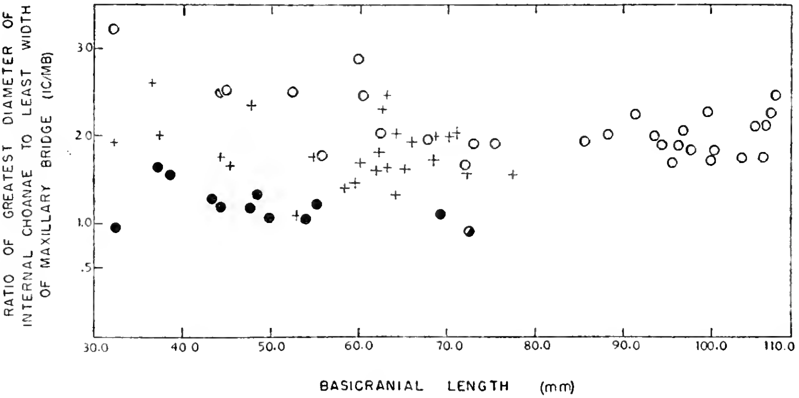


FIG. 20. Basicranial length and ratio of greatest diameter of internal choanae to least width of maxillary bridge (IC/MB) on 30 skulls of *T. ferox* (open circles), 26 of *T. spinifer* (crosses), and 12 of the *agassizi*-form (solid circles; half shaded circle represents holotype of *agassizi*). Skulls of the *agassizi*-form tend to have slightly smaller internal choanae than those of *spinifer* or *ferox*.

with the submarginal ring"; I examined this specimen and noted that it had only one dark marginal line. Stejneger (*op. cit.*:64) mentioned another from the Pearl River drainage, and Crenshaw and Hopkins (1955:20) wrote that some individuals from Georgia have only one dark marginal line. Presumably MCZ 1606 (now in the Albany Museum) recorded by Stejneger (*op. cit.*:52) as *Amyda s. spinifer* from Columbus, Georgia, is another specimen.

Some skulls of soft-shelled turtles from streams of the Atlantic Coast drainage, including the skull of the holotype of *Platypeltis* (= *Trionyx*) *agassizi* Baur (MCZ 37172, Pl. 54), show at least two differences from other skulls of *asper* and from those of other subspecies of *T. spinifer.* Figure 20 shows that skulls of *agassizi* tend to have slightly smaller internal choanae (ratio IC/MB) than those of *T. spinifer* and *T. ferox;* there is seemingly little difference between skulls of *ferox* and *spinifer,* and little, if any, ontogenetic variation. Figure 21 shows that most skulls of the *agassizi*-form that exceed 43.0 millimeters have a more expanded, alveolar surface of the maxilla than skulls of *spinifer* of approximately the same size; most skulls exceeding a basicranial length of 43.0 millimeters, and certainly all skulls exceeding 50.0 millimeters are those of females. Stejneger (1944:Pl. 30) also has provided photographs of a skull of the *agassizi*-form. It is of interest that of the 12 *agassizi*-form skulls (MCZ 37172; USNM 8708, 029034, 51981, 66859, 71681, 91282, 91310-11, 92521, 92583-84) that I examined some resemble *ferox* (Neill, 1951:9) in having the alveolar surfaces of the jaws broadened, and the greatest width at the level of the quadratojugal (Table 3, Plate 54); also, the localities of all 12 skulls are within the geographic range of *ferox.* Skulls of *ferox,* however, have conspicuously broadened alveolar surfaces of the jaws only when they exceed in length the largest skulls of *agassizi.* The differences of skulls of the *agassizi*-form possibly reflect isolation in the Atlantic Coast drainage, and an adaptation in feeding habits. So far as I can ascertain, individuals occurring in rivers of the Atlantic Coast drainage in Georgia and South Carolina (referable to *agassizi*) do not differ consistently in external characters from individuals of *T. s. asper* that occur westward in the Apalachicola drainage.

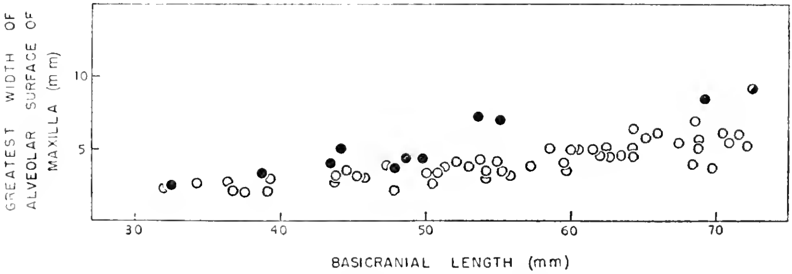


FIG. 21. Basicranial length and greatest width of alveolar surface of maxilla on 52 skulls of *T. spinifer* (open circles) and 11 of the *agassizi*-form (solid circles; half shaded circle represents holotype of *agassizi*). Most skulls of the *agassizi*-form that exceed 43 mm. in basicranial length have a more expanded, alveolar surface of the maxilla than skulls of *spinifer* of approximately the same size. All skulls exceeding 50 mm. are those of females.

Comparisons.—*Trionyx s. asper* can be distinguished from all other subspecies of *T. spinifer* by usually having more than one black line paralleling the rear margin of the carapace. This character and the frequent fusion of the postlabial and postocular stripes on the side of the head distinguish *asper* from *spinifer* and *hartwegi*. *T. s. asper* differs from *pallidus, guadalupensis* and *emoryi* in having blackish spots and ocelli on the carapace, and lacking whitish dots or tubercles. *T. s. asper* resembles *spinifer, hartwegi* and *pallidus* but differs from *guadalupensis* and *emoryi* in having conical tubercles along the anterior edge of the carapace in large females. For additional differences see accounts of other subspecies.

Of the subspecies of *T. spinifer*, *asper* has a proportionately wide head that is closely approached in the subspecies *guadalupensis* and *emoryi; T. s. asper* differs from *guadalupensis* and *emoryi* in having a wider carapace, and resembles *hartwegi* and *spinifer,* but differs from the other subspecies in having the carapace widest at a plane approximately one-half way back on the carapace. *T. s. asper* differs from the other subspecies in having the shortest plastron.

Remarks.—Stejneger (1944:72-74) has discussed the history of Baur's *Platypeltis agassizi.* Briefly, Agassiz's description of *Platypeltis ferox* wherein he (1857:402) states that "The young ferox [Pl. 6, fig. 3] has two or three concentric black lines separating the pale margin . . .," was applicable to *T. s. asper.* Agassiz mentioned also that the young of his *Aspidonectes asper* (*op. cit.*:406) "as in Platypeltis ferox, . . . has . . . two or three black lines separating the pale rim of the posterior margin, . . ."; however, *A. asper* was distinguished chiefly by the ". . . prominent warts of the bony plates (*loc. cit.*)." Because the description of the pattern of *ferox* resembled that of *asper*, the validity of *asper* was not agreed upon by all workers. Boulenger (1889:245, footnote 1) referred to *asper* as a species that required ". . . further investigation."

Baur (1888:1121) realized that Agassiz's description of *ferox* was not that of *Testudo ferox* Schneider, and regarded the description of Agassiz as applying to a new species, which he named *Platypeltis agassizii;* Baur (*op. cit.*:1122) also recognized *asper,* referring it to the genus *Aspidonectes.* Baur designated a specimen from Georgia (the only individual seen by him) as the type of *agassizi* (Stejneger, *op. cit.*:73, footnote); this specimen is now MCZ 37172. Five years later (1893:218), Baur discussed generic relationships of trionychids, seemingly only on the basis of skulls (holotype of *agassizi* not mentioned), and referred *agassizi* to the resurrected genus *Pelodiscus* Fitzinger, 1835, which was distinguished from the other two American genera that Baur recognized (*Platypeltis* and *Amyda*) by having the "Posterior nares reduced in size by the inner and posterior extension of the maxillaries." Baur also transferred *asper* to the genus *Platypeltis,* and restricted the type locality of that species to "Lake Concordia, La." (*op. cit*:220); the type locality of *agassizi* was restricted to "Western Georgia" (*loc. cit.*).

The name-combination, *Pelodiscus agassizi,* was not generally accepted. Hay (1892:144) and Siebenrock (1924:188) referred *agassizi* to the genus *Trionyx.* Hay regarded *agassizi* as a full species (see discussion by Stejneger, 1944:73), whereas Siebenrock considered it a subspecies of *spiniferus;* both authors regarded *asper* as a synonym of *agassizi.* Neither *asper* nor *agassizi* was mentioned in the first three editions of the Check List of North American Amphibians and Reptiles (Stejneger and Barbour, 1917, 1923, 1933); the same authors in the fourth (1939:171, 172) and fifth editions (1943:212, 213) listed *agassizi* as a full species, and *asper* as a subspecies of *spinifera.* Stejneger (1944) used the same arrangement as set forth in the fourth and fifth editions of the Check List, and distinguished *agassizi* on the basis of cranial characters, namely, the small size of the internal choanae, the greater width of the alveolar surface of the lower jaw, and the position of the suture between the palatine and basisphenoid relative to the posterior edge of the temporal fossa. Neill (1951:9) regarded the peculiarities of the *agassizi*-type skull as inconstant, but recognized *agassizi* (and *asper*) as a subspecies of *ferox.* Crenshaw and Hopkins (1955) showed that *asper* did not intergrade with *ferox.* Schwartz showed that *agassizi* did not intergrade with *ferox,* and regarded *agassizi* as a synonym of *T. s. asper* (1956:17), but stated that *agassizi* possessed "wider crushing surfaces on the maxillae than does *T. s. asper,* even when skulls of the same size and sex are compared" (*op. cit.*:9).

The holotype of *Platypeltis agassizi* (MCZ 37172) is a dried adult female consisting of shell, skull and limb bones; the carapace is approximately 300 millimeters long (Schwartz, *loc. cit.*). I have examined only the skull of MCZ 37172 (Plate 54), and it is the largest of 12 *agassizi*-type skulls I have seen. The basicranial length is 72.5 millimeters, and the greatest width, which occurs at the level of the quadratojugals, is 52.9 millimeters. The *agassizi*-type skulls have been discussed under the subsection on variation.

The type locality of *T. s. asper,* Lake Concordia, Louisiana (lower Mississippi River drainage) as restricted by Baur (1893:220), is in an area of intergradation of three subspecies of *Trionyx spinifer* where most individuals are not typical of *asper.* The syntypes, the designation of MCZ 1597 as a lectotype, and Pearl River, Columbus, Marion County, Mississippi, as the type locality have been discussed elsewhere (Webb, 1960).

The range of *T. s. asper* overlaps that of *T. ferox* in Georgia and South Carolina. The two species remain distinct in the area of overlap of their geographic ranges (Crenshaw and Hopkins, 1955:16; Schwartz, *op. cit.*:5). *Trionyx s. asper* intergrades with *T. s. hartwegi* and *T. s. spinifer* in the lower Mississippi Valley (Conant and Goin, 1948:11).

However, there are few specimens available that indicate intergradation of *asper* with the *spinifer-hartwegi* complex in the lower Mississippi River drainage; this may be due to the fact that *asper* inhabits waterways that do not drain into the Mississippi River. Perhaps intergradation is more prevalent than the morphological basis that I have relied upon indicates; in any event, there are few specimens that have more than one dark marginal line (which is the only character that is unique for *asper*) from the lower Mississippi drainage. A young male (TU 11928.9) from Bayou Gauche between Paradis and Des Allemands, St. Charles Parish, Louisiana, has a pattern on the carapace resembling that of *asper;* several other small softshells (TU) are available from the same locality but none shows more than one dark marginal line. Another specimen (USNM 95192), a young female from a barrow pit of the Big Black River (Mississippi River drainage), Madison County, Mississippi, resembles *asper* in having more than one marginal ring. Of three large females from Moon Lake, an oxbow of the Mississippi River in Coatopa County, Mississippi (AMNH 5285-86, 5289), only 5289 shows evidence of two marginal lines. USNM 73669 (Greenwood, LeFlore County, Mississippi) also indicates intergradation in that the spots tend to be linear just inside the dark marginal line, but the specimen more closely resembles the *hartwegi-spinifer* complex rather than *asper.*

There seems to be little adumbration of the dark marginal lines of *asper* in populations from the lower Mississippi River drainage. Blackish spots and ocelli vary in size and there are many kinds of pattern on the carapace. Soft-shelled turtles inhabiting the Mississippi River and its tributaries in Louisiana and Mississippi certainly represent an intergrading population of *spinifer* and *hartwegi,* and, to a lesser extent, of *asper.* Soft-shelled turtles inhabiting the Pearl River drainage and rivers that drain into Lake Pontchartrain immediately adjacent to the east are predominantly *asper.*

Specimens having localities from the Pearl River and Lake Pontchartrain drainages are listed under the account of *asper* and are referred to that subspecies on the distribution map; specimens from the Mississippi drainage in Mississippi are referred to *spinifer.*

One specimen (UMMZ 59198, Bradley County, Tennessee), from the Tennessee River drainage where *T. s. spinifer* occurs, deviates markedly from *spinifer* and suggests intergradation. UMMZ 59198, plastral length 4.8 centimeters, has ocelli in the center of the carapace only two millimeters in diameter, a distinct but interrupted, second marginal ring consisting of spots, and the pale postlabial and postocular stripes in contact on both sides of the head.

Specimens examined.—Total 110, as follows: ALABAMA: *Barbour:* UMMZ 113038, Chattahoochee River, Eufala. *Cherokee:* ANSP 24592, "near" center of Terrapin Creek. *Conecuh:* UMMZ 70736, Murder Creek, Castleberry. *Escambia:* TU 15823, Escambia River, 1 mi. N Sardine; UMMZ 70734, Escambia River at Flomaton. *Henry:* TU 15630, 3 mi. NW jct. Echo Farm Rd. and Rt. 136 on Echo Farm Rd. *Lowndes:* UMMZ 67759, Pintlalla Creek. *Mobile:* MCZ 1608 (2), 1608A, Mobile. *Sumpter:* USNM 83996, 3 mi. SE Coatopa. *Tuscaloosa:* TU 14673 (5), Black Warrior River, 17.5 mi. SSW Tuscaloosa; UA 52-1085, Cottondale. *Walker:* KU 50843, 50851, TU 17137, Mulberry Fork, Black Warrior River, 9 mi. E Jasper.

FLORIDA: *Calhoun:* KU 50837-38, Chipola River, 4 mi. N Scott's Ferry; TU 16689 (4), Chipola River "near" Blountstown. *Escambia:* TU 13474, 15869 (3), 16584, Escambia River, 1.2 mi. E Century. *Okaloosa:* TU 15661, Blackwater River, 4.3 mi. NW Baker on Route 4. *Santa Rosa:* AMNH 44621, Blackwater River, Milton. *Walton:* UMMZ 110421, Pond Creek, 4 mi. SW Florala, Covington County, Alabama.

GEORGIA: *Baker:* TU 15889 (3), USNM 134243-48, Flint River "near" Newton; USNM 30822. *Baldwin:* USNM 8708, Milledgeville. *Bryan:* TU 15090, Canouche River, 2.3 mi. W Groveland. *Chatham:* USNM 51981, 92583-84, Savannah. *Chattooga:* UMMZ 113037, tributary of Chattooga River, Lyerly. *Decatur:* KU 50839-42, Flint River, 1.5 mi. S Bainbridge. *Fulton:* UMMZ 53037, Roswell. *Lincoln:* USNM 91282-83, above Price Island, Savannah River. *Murray:* UMMZ 59196, 9 mi. N Spring Place. *Pulaski:* TU 14882, Ocmulgee River, 4.3 mi. SE Hawkinsville. *Richmond:* USNM 66859, Augusta. *Whitfield:* UMMZ 74209, Cohulla Creek, Prater's Mill "near" Dalton. *County unknown:* MCZ 37172; UMMZ 109864, Flint River at mouth of Dry Creek; USNM 029034.

LOUISIANA: *East Baton Rouge:* LSU 11, 1643-44, City Park Lake in Baton Rouge; TU 17237, Amite River "near" Baton Rouge. *St. Tammany:* TU 6356, headwater creek of Bayou Lacombe; TU 16071, USNM 66147, mouth of Tchefuncta Creek in Lake Pontchartrain. *Tangipahoa:* TU 13623, 3.1 mi. W Hammond; USNM 68054, Robert. *Washington:* KU 50840, 50846, TU 17117, Pearl River at Varnado. *Parish unknown* (East Baton Rouge or Tangipahoa): UMMZ 95614, Manchac.

MISSISSIPPI: *Chickasaw:* USNM 115981, Chookatonkchie Creek. *Clarke:* USNM 79350-51, 1 mi. W Melvin, Choctaw County, Alabama; USNM 100805, Enterprise. *Forrest:* WEB 55-586, 1 mi. S Hattiesburg. *Hancock:* AMNH 46780; WEB 54-651, Hickory Creek "near" Kiln. *Lauderdale:* UMMZ 74681, 9 mi. W Meridian; UMMZ 90130, Lake Juanita, 15 mi. W Meridian. *Lawrence:* KU 47120, TU 17307.1, Pearl River, 9 mi. S Monticello; USNM 7653-54, Pearl River at Monticello. *Lee:* CM 31904, Verona; USNM 115979, Cower's Area near Guntown. *Madison:* USNM 95191, 95193-94, Pearl River. *Marion:* MCZ 1597, Pearl River at Columbus (designated type locality). *Pearl River:* CM 21100, Pearl River, 20 mi. W Poplarville; TU 14362, Hobolochito Creek, 1 mi. N Picayune. *Perry:* WEB 55-580, Beaver Dam Creek, 1 mi. N Richton. *Walthall:* KU 50844, Bogue Chitto River, Dillon.

SOUTH CAROLINA: *Abbeville:* USNM 7650, Abbeville? (reported by Pickens, 1927:113; locality considered in error by Stejneger, 1944:50; USNM 7650 having only one dark marginal line paralleling rear margin of carapace is possibly an aberrant specimen—see page 495 of present account). *Greenwood:* USNM 71681, 73668, Greenwood. *McCormick:* USNM 91310-12, Savannah River, 5 mi. W Plum Branch; USNM 92521, near Parksville. *Richland:* AMNH 70724-25, Broad River, Columbia.

NO DATA: USNM 8359 (erroneously reported from Madison, Indiana by Yarrow, 1882:29 and Hay, 1892:145; see discussion by Cahn, 1937:200, and Stejneger, 1944:73-75); USNM 131859.

Records in the literature.—ALABAMA: *Coffee:* Elba (KKA). *Marengo:* Tombigbee River near Demopolis. *Mobile:* Fig Island (Löding, 1922:47).

FLORIDA: *Jackson:* Chattahoochee River, 8 mi. SE Butler. *Leon:* Ochlocknee River, NW of Tallahassee (Goin, 1948:304).

GEORGIA: *Bartow:* Etowah River below Allatoona Dam, *ca.* 4 mi. ESE Cartersville (Crenshaw and Hopkins, 1955:15). *Berrien:* (Knepton, 1956: 324). *Emanuel:* Ogeeche River (Schwartz, 1956:19). *Fulton:* Nancy Creek, Atlanta (Dunston, 1960:278). *Gwinnett: Irwin:* (Knepton, *loc. cit.*). *Jenkins:* Ogeeche River near Buckland Creek jct., 2.5 mi. S Millen. *Liberty:* Camp Stewart, 4 mi. N Hinesville. *Morgan:* Lake Rutledge (Schwartz, *loc. cit.*). *Muscogee:* Columbus (Stejneger, 1944:52). *Wayne:* Altamaha River, 5 mi. N Mt. Pleasant (Schwartz, *loc. cit.*). *Wilcox:* Ocmulgee River, 3-4 mi. SSE Abbeville (Crenshaw and Hopkins, *op cit.*:16, footnote; Schwartz, *loc. cit.*).

MISSISSIPPI: *George:* Whiskey Creek (Cook, 1946:185). *Harrison:* near Biloxi. *Jackson:* Pascagoula Swamp, *ca.* 40 mi. E. Biloxi (Corrington, 1927: 101). *Jones:* Eastabuchie. *Lee:* Cain Creek Bottom. *Lincoln:* Old Brook Creek. *Lowndes:* Tombigbee River, Camp Henry Pratt and Columbus; Lake Park, Columbus. *Pearl River:* 21 mi. SW Poplarville; 10 mi. W Poplarville; 4 mi. W Poplarville. *Wayne:* Trigg Area (Cook, *loc. cit.*).

NORTH CAROLINA: *Mecklenburg:* Catawba River near Charlotte (Schwartz, 1956:20).

SOUTH CAROLINA: *Aiken:* Savannah River, 10 mi. SW Jackson. *Allendale:* Savannah River, Fennell Hill, 2 mi. S US 301. *Anderson:* Pendleton. *Bamberg:* South Edisto River, Cannon's Bridge, 5 mi. from Bamberg. *Berkeley:* 2.5 mi. W Pinopolis. *Charleston:* Charleston. *Clarendon:* Upper Lake Marion at US 301; Lake Marion, 13 mi. SW Manning; 3.3 mi. S Jordan; 6.3 mi. S Jordan; Wyboo Creek, 8.5 mi. from Manning. *Colleton:* Edisto River (Schwartz, 1956:19-20). *Darlington:* Pee Dee River, Society Hill (Stejneger, 1944:72). *Dorchester:* Edisto River, 17 mi. from Summerville; Edisto River, 14 mi. W Summerville; Edisto River, 2.5 mi. S Hart's Bluff. *Fairfield:* 1 mi. N Peak, Newberry County. *Georgetown:* North Santee River, 1 mi. above US 17. *McCormick:* Little River near McCormick; Little River, 3 mi. NE Mt. Carmel. *Laurens:* Enoree River, 3 mi. S Cashville, Spartanburg County; Enoree River, 9.4 mi. N Clinton. *Orangeburg:* Edisto River, Orangeburg. *Saluda:* Batesburg; Lake Murray; Little Saluda River; 5 mi. from Saluda. *County unknown:* Upper Lake Santee (Schwartz, *loc. cit.*).

Trionyx spinifer emoryi (Agassiz)

Texas Spiny Softshell

Plates 43, 44

Aspidonectes emoryi Agassiz (in part), Contr. Nat. Hist. United States, Vol. 1, Pt. 2, p. 407; Vol. 2, Pt. 3, pl. 6, figs. 4-5, 1857.

T[rionyx] s[pinifer] emoryi Schwartz, Charleston Mus. Leaflet, No. 26, p. 11, 1956.

Type.—Lectotype, USNM 7855; alcoholic (sex undetermined); obtained from the Río Grande near Brownsville, Texas, in the course of the Mexican Boundary Survey under the command of Colonel Wm. H. Emory.

Range.—Southwestern United States and northern México; the Río Grande drainage in Texas, New Mexico and northern México; the Río San Fernando and Río Purificación drainages in northeastern México; the Colorado River drainage in Arizona, New Mexico, and southern Nevada (see map, Fig. 19).

Diagnosis.—Juvenal pattern of white dots, not encircled with dusky or blackish ocelli, confined to posterior third of carapace; pale rim of carapace conspicuously widened, four to five times wider posteriorly than laterally; a dark triangle in front of eyes, base line connecting anterior margins of orbits; pale postocular stripe interrupted leaving conspicuous pale, usually dark-bordered, blotch just behind eye.

Description.—Plastral length of smallest hatchling, 2.5 centimeters (USNM 7632); of largest male, 13.0 centimeters (KU 2914, 3125, 3150); of largest female, 22.0 centimeters (TNHC 8023, 8104).

Carapace pale brownish or tan, lacking whitish dots on anterior half; whitish dots confined to posterior third of carapace, sometimes lacking posteriorly, especially on juveniles; small, blackish dots rarely occurring on surface of carapace, usually confined to margins when present; pale rim of carapace four to five times wider posteriorly than laterally.

Pattern on snout rarely variable, consisting of pale stripes extending forward from eyes that have only their outer borders darkened and a straight or slightly curved, dark line that connects anterior margins of orbits; few, if any, dark markings in subocular and postlabial region; pattern on side of head having few contrasting marks, often of nearly uniform coloration; postocular stripe usually interrupted; anterior segment of postocular stripe just behind eye usually dark-bordered; posterior segment usually not dark-bordered or sharply distinguished from background; pattern on dorsal parts of soft parts of body contrasting, of relatively small dark marks; dark streaks often coincident with digits.

Underparts whitish, occasionally having blackish dots or smudges on posterior part of carapace, in region of bridge, or on lateral parts of chin and throat; few dark marks often on webbing of limbs and on palms and soles.

Small, flattened or wartlike, tubercles that occasionally have sharp tips along anterior edge of carapace on adult males; tubercles flattened, scarcely elevated, never conical along anterior edge of carapace on large females; whitish, knoblike tubercles often present posteriorly in middle of carapace and in nuchal region on large females; mottled and blotched pattern sometimes contrasting on carapace of large females; whitish dots of juvenal pattern often visible through overlying blotched pattern of large females.

Ontogenetic variation in PL/HW, mean PL/HW of specimens having plastral lengths 7.0 centimeters or less, 3.68, and exceeding 7.0 centimeters, 5.19; ontogenetic variation in CL/CW, mean CL/CW of specimens having plastral lengths 8.5 centimeters or less, 1.17, and exceeding 8.5 centimeters, 1.27; mean CL/PCW, 2.18; mean HW/SL, 1.43; mean CL/PL, 1.37.

Variation.—Ten topotypes (six males, three females, one juvenile) from Brownsville, Texas (BCB 7465-73, 7564), have the following characteristics: pale rim widened posteriorly as described above; females (plastral lengths 9.8, 10.2 and 11.7 cm.) having blackish marks in pale rim, which are absent in males of corresponding size; interrupted postocular stripe with pale blotch behind eye; postocular pale blotch having blackish borders or not; dark triangular mark on snout in front of eyes; white dots present only on posterior third of carapace; carapace of females grayish, blotched pattern not contrasting; carapace of males paler, greenish-gray; undersurface immaculate except 7468 and 7472 that have blackish flecks at bridge and, on 7472, blackish marks that extend posteriorly onto ventral surface of carapace; tubercles along anterior edge of carapace flattened and rounded in adult males, more knoblike in females; largest specimen, BCB 7472, female, plastron 11.7 centimeters long.

T. s. emoryi varies more than any other subspecies of *Trionyx spinifer.* A large series of males and females (KU) from the Salt River (Colorado River drainage), near Phoenix, Arizona, is characterized by many adult males having indistinct white dots on posterior half of carapace; blotching on carapace of females of contrasting lichenlike figures, but usually non-contrasting and pale brownish or tan; pale rim of carapace distinct from ground color of carapace in largest female (KU 2905, plastron 21.5 cm. in length), but having dark or dusky markings: dark interorbital stripe often lacking. AMNH 58370 (Nevada) and UMMZ 92006 (Arizona) also have the dark line connecting the anterior margins of the orbits interrupted; seemingly the dark interorbital line is most often interrupted in those softshells inhabiting the Colorado River system of Nevada and Arizona.

Other variant individuals are: TU 14453.2, 14462 and 3696 having the plastron extending slightly farther forward than the carapace, thus resembling *T. ferox;* UMMZ 54021 and CNHM 39999, hatchlings, lacking distinct whitish dots on posterior half of carapace; UI 43509 and KU 39991 having stained (brown or blackish) claws; and, CNHM 6810, an adult male, lacking a spinose (sandpapery) carapace. I am unable to discern geographic variation in these or other characters.

The ground color of the carapace on some individuals from the Pecos River (TU, Terrell County, Texas) is grayish and in contrast with the pale rim (Pl. 44). UI 43509 from the Río Florida, La Cruz, Chihuahua, a female, has a dark brownish carapace with little evidence of a blotched pattern execpt on the pale rim of the carapace. A female and adult male from the Río Sabinas, Coahuila (MSU 905-06), also show considerable darkening on the dorsal surfaces; the pale rim is evident but not in sharp contrast to the coloration of the carapace. Notes taken on the freshly-killed Sabinas individuals are: male—carapace olive-gray; dorsal surface of soft parts of body olive-green to grayish, a bright yellow suffusion on limbs and neck; female—carapace and soft parts of body dark olive, laterally pale yellow; the plastron extends slightly farther forward than the carapace in both sexes.

Notes on coloration (judged to be the most common or "normal" type) of living *emoryi* from the Río Mesquites, central Coahuila, are: Adult male (KU 53753)—pale rim butterscotch yellow; marginal line blackish; whitish dots on pale brown or tan carapace; soft parts of body olive or olive-green, slightly darker on head and paler (yellowish) on hind limbs; pale areas on side of head pale yellow, having tint of orange on neck; ventral surface white, yellow laterally on neck. Adult female (KU 53754)—carapace having contrasting blotched and mottled pattern of pale browns and tans; soft parts of body olive brown, darker brown blotching on head; dorsal surface of limbs olive-green having pale areas lemon yellow and webbing butterscotch yellow; side of neck and head, chin and throat pale lemon yellow; ventral surface white having slight red tinge to groin and soft parts posteriorly; underside of carapace near edge pale yellow.

Softshells from the Río Grande in the Big Bend region of Texas, and the Río Conchos in Chihuahua differ from other specimens of *emoryi*. Fifteen adult males, KU 51187-201 (no females in sample), were taken from the mouth of the Río San Pedro at Meoquí, Chihuahua (see KU 51194, Pl. 44). They are noteworthy because of a conspicuous orange or orange-yellow on the side of the head. Another relatively consistent character is the blackish tip of snout (excepting 51199), although the degree (palest on 51190) and extent of pigmentation posteriorly on the snout is variable. Eleven males, KU 51175-85, from approximately 100 miles northeastward in the Río Conchos near Ojinaga, Chihuahua, also have the bright orange on the side of the head; the tip of the snout is not blackish, although in some it is slightly darkened. Three females, KU 51174, 51186 (from Ojinaga) and 51173 (from 8 mi. S, 16 mi. W Ojinaga), lack the orange on the side of the head; KU 51186 has a plastral length of 8.0 centimeters, whereas the other two females have the same plastral length of 16.5 centimeters (larger than any male). Nineteen adult males, KU 51965-72, 51980-90, from the Río Grande near Lajitas also have the orangish coloration on the side of the head, whereas twenty females, KU 51954-64, 51973-79, 51991-92 (three smaller than largest male) lack the coloration. The tip of the snout is not blackish on any turtle in the series from Lajitas. The smallest female, from Lajitas, having a plastral length of 6.9 centimeters, has a mottled carapace.

The orange of males is most conspicuous in the pale postocular and postlabial areas; the stripes of the snout (distally) and the color of the neck at its juncture with the immaculate ventral surface are orange-yellow. The orange coloration is confined to males (all examined were sexually mature) and is probably not of seasonal occurrence (see comments under secondary sexual variation). I have not noticed this coloration in other males of the subspecies *emoryi;* however, long-preserved males might be expected to lack the orange color; the specimens mentioned above were initially preserved in alcohol. KU 51179 (plastral length 8.2 cm., from Ojinaga) is the smallest sexually mature male of the species *spinifer* that I have seen. Another character of note is the generally greater development of the plastral callosities (resembling *muticus*) than in other subspecies of *spinifer* or specimens of *emoryi;* three small adult males (KU 51177, 51990, 51987, plastral length 9.3, 9.9 and 9.1 cm., respectively) have large hyoplastral and hypoplastral callosities that appear to touch medially, and callosities on the epiplastron and both preplastra.

On July 8, 1953, an adult male of *T. spinifer* was removed from a hoopnet set in the Río Purificación at Padilla, Tamaulipas, México. I was particularly impressed by the lack of whitish dots on the dark carapace; the following notes were taken from the freshly-killed specimen: carapace a uniform dark olive, lacking white dots and having a yellowish rim widest posteriorly; tubercles on anterior edge of carapace only slightly raised, inconspicuous; top of head olive with few dots and streaks; a well-defined yellowish postocular stripe not conspicuously interrupted; sharp contrast between dark olive on side of head and pale ventral coloration; yellowish-orange ventrolaterally on head; an uninterrupted slightly-curved line connecting the anterior margins of the orbits; carapace pear-shaped; underparts whitish, lacking markings. This specimen has since been destroyed. The only other specimen I have seen from this locality is a hatchling (UMMZ 69412, Pl. 43), which has a pale brownish or tan carapace that lacks whitish dots; it resembles *emoryi* in other characters. Although the absence of whitish dots is not distinctive, its combination with the uniform dark olive carapace in adult males and the fact that the Río Purificación is an isolated drainage system, suggests that soft-shelled turtles from that river system may warrant further taxonomic study.

Comparisons.—From all other subspecies of *spinifer, T. s. emoryi* can be distinguished by having a pale rim on the carapace that is four to five times wider posteriorly than it is laterally. This character, unique for *emoryi,* combined with patterns on the snout, side of head and carapace that are subject to little variation, permit ready identification of the subspecies *emoryi. T. s. emoryi* resembles *pallidus,* and *guadalupensis* and differs from *spinifer, hartwegi* and *asper* in having whitish tubercles or dots on the carapace. *T. s. emoryi* resembles *guadalupensis* but differs from *pallidus, spinifer, hartwegi* and *asper* in lacking conical tubercles along the anterior edge of the carapace on large females. For additional differences see accounts of other subspecies.

Some populations of *T. s. emoryi* resemble *T. muticus* in the size at which sexual maturity is attained and in the development of the plastral callosities. *T. s. emoryi* has a wide head that resembles that of *T. ferox, T. ater, T. s. asper* and *T. s. guadalupensis; T. s. emoryi* also resembles *T. ferox* and *T. ater* but differs from the other subspeceis of *T. spinifer* and *T. muticus* in having a narrower carapace. *T. s. emoryi* resembles *T. s. guadalupensis, T. s. pallidus* and *T. ater,* and differs from the other subspecies of *spinifer* and *T. muticus,* in having the carapace widest farther posteriorly than one-half way back on the carapace. *T. s. emoryi* resembles *T. ferox* in having the shortest length of snout of the subspecies of *spinifer.* The plastron is shorter than in *T. ferox,* longer than in *T. s. asper,* and about the same length as in *T. muticus* and the other subspecies of *T. spinifer.*

Remarks.—Agassiz (1857, 1:407-08) did not designate a holotype in the original description of *Aspidonectes emoryi;* specimens are mentioned from the lower Río Grande of Texas, near Brownsville, and a stream of the Río Brazos drainage in Williamson County, Texas. The description is applicable to *T. s. emoryi* as herein restricted, except for the statement that the white tubercles of young specimens are "encircled by faint black lines."; that statement is presumably based on the juveniles from Williamson County. *T. s. emoryi* does not occur in Williamson County, Texas. Barbour and Loveridge (1929:225) listed MCZ 1909-10 and 1627 as cotypes. Stejneger (1944:65) mentioned MCZ 1909, 1913 and USNM 7855 as cotypes; the legend for Plate 20 (*op. cit.*) refers to a drawing that "corresponds fairly closely with the type (MCZ 1910) collected at Brownsville, Texas, by Col. Emory."

The syntypic series consists of seven specimens—MCZ 1627 (two specimens) from Williamson County, Texas; MCZ 1909 (three specimens) and 1910 from Brownsville, Texas; and USNM 7855 from Brownsville, Texas. The listing of number 1913 by Stejneger is considered a *lapsus* for 1910 as MCZ 1913 is catalogued as a *Graptemys geographica* (in letter dated November 17, 1959 from Dr. Ernest E. Williams). Stejneger's reference to MCZ 1910 as the type is considered unintentional and an inadequate designation of a lectotype.

In the "remarks" column of the USNM museum catalog, number 7855 is referred to as "Ag. Type." USNM 7855 is here designated as lectotype of *Trionyx spinifer emoryi*. The lectotype is a young specimen (female?) that is not easily sexed by external characters; the plastron measures (in centimeters) 6.3 in length, the carapace 8.2 in length and 7.0 in width, and the head 1.4 in width. The carapace is pale brown having inconspicuous whitish dots posteriorly and a pale rim that is approximately 6.8 times wider posteriorly (4.1 mm.) than it is laterally (0.6 mm.). The slightly curved dark line connecting the anterior margins of the orbits is dimmer than the dark lines that extend forward from the eyes. The pale postocular stripes having blackish, dotted borders are interrupted; there are no other markings on the side of the head. The ventral surface is immaculate except for a few dark dots on the right side of the carapace; the ground color is pale brown or tan, but the upper layer of skin can be scraped away revealing an underlying pale lavender-cream ground color. The tubercles along the anterior edge of the carapace resemble small rounded warts.

MCZ 1910 is an adult male *T. s. emoryi* having a plastron 10.7 centimeters in length. The carapace is pale brown having a relatively smooth anterior edge, inconspicuous whitish tubercles posteriorly, and a pale rim five times wider posteriorly than laterally; the pattern on the head resembles that of *emoryi*.

Each of three hatchlings of *T. s. emoryi*, 3.4, 3.5 and 3.9 centimeters in plastral length, bears an MCZ catalogue number of 1909. The carapaces are dark tan or gray having pale rims 3.7, 5.2 and 5.2 times wider posteriorly than laterally, and white dots absent or obscure posteriorly; two specimens have small blackish dots paralleling the pale rim posteriorly. The patterns on the heads are referable to *emoryi*.

The two juvenal syntypes (5.2 and 6.1 cm. in plastral length) from Williamson County, Texas, are both catalogued as MCZ 1627, but only one of these bears a catalogue number. The two softshells are not *emoryi*, and are more nearly like *T. s. guadalupensis* than *T. s. pallidus*. Actually, they are from an area of intergradation between those subspecies (see comments concerning intergradation under the accounts of the subspecies *pallidus* and *guadalupensis*). White spots occur on the carapaces anteriorly and posteriorly, the larger (more posterior) of which are encircled with dusky ocelli. The carapace of the small specimen (bearing no number) is brown having a few, small black specks intermixed with the white spots. The carapace of the large specimen is pale lavender and has a more obscure pattern than the other specimen.

After Agassiz's description, *emoryi* was accepted as a distinct species. Neill (1951:15) suggested that *emoryi* was subspecifically related to *T. ferox*. Crenshaw and Hopkins (1955) and Schwartz (1956), however, demonstrated that *ferox* was a distinct species; *emoryi* has since been considered a subspecies of *T. spinifer*.

Two specimens having blackish dots on the carapace, indicate relationship with *T. s. guadalupensis.* USNM 7638, a hatchling, has large whitish dots surrounded by blackish dots confined to the posterior half of the carapace, and the locality for this specimen is merely Río Bravo (= Río Grande). CNHM 47366, a hatchling from Sierra de las Palmas (Sierra de Santa Rosa, La Palma), Coahuila, has a few, small, blackish dots, irregularly spaced, on the anterior half of the carapace, but other dots more evenly distributed on the posterior half where they are intermixed with whitish dots. The drawing of the dorsal view of a hatchling *emoryi* (Agassiz, 1857:Pl. 6, Fig. 4) shows a sprinkling of blackish dots on the anterior half of the carapace. A hatchling from Eagle Pass (USNM 116578) does not have a noticeably widened pale rim posteriorly on the carapace, and is not distinguishable from *pallidus.* See account of *T. s. guadalupensis* for further comments on intergradation.

A soft-shelled turtle that was obtained in the Sacramento River by three fishermen, near Sacramento, California, was named *Aspidonectes californiana* by Rivers (1889:233). A comparison (with *Aspidonectes spinifer* and *A. emoryi*) of certain features of the skull was largely prepared by Baur and included in the description (*op. cit.*:234-35); seemingly, the most trenchant character of the skull of *californiana* was the enlarged alveolar surfaces of the jaws. This feature prompted Baur (1893:220) to refer *californiana* to the genus *Pelodiscus,* which also included *agassizi* (skulls also having jaws with enlarged alveolar surfaces) and several Old World species. Van Denburgh (1917) discussed the origin of the specimen that formed the basis of River's description and concluded that it was brought over from China. Siebenrock (1924:192) and Mertens and Wermuth (1955:389) listed *Aspidonectes californiana* as a synonym of *emoryi.* River's description is not that of *emoryi;* the enlarged alveolar surfaces of the jaws, and the dark carapace having tubercular ridges suggest a resemblance to *T. ferox.* The papillae on the neck are not found in any American species. Miller (1946:46, footnote 2) believed that "it obviously was introduced, apparently from China," and cited Pope (1935:61), who declared the specimen to represent *Trionyx sinensis.*

Schmidt (1924:64) first reported the occurrence of *T. s. emoryi* west of the continental divide in Arizona and suggested that it was highly probable that the species had been introduced near Phoenix in recent years. Cowles and Bogert (1936:42) mentioned a species of softshell occurring in the Boulder Dam region and presumed the species to be native to Asia and introduced by the Chinese. Linsdale and Gressitt (1937:222) determined the status of the species in the Colorado River drainage as *T. s. emoryi.* The discussions by Dill (1944:179-81) and Miller (1946:46) indicate that *emoryi* was introduced into the Gila River (Colorado River drainage) in western New Mexico near the turn of the century.

T. s. emoryi and *T. ater* are the only kinds of softshells occurring in México. The colloquial name for soft-shelled turtles in México is "tortuga blanca." This name is also used in reference to the Central American river turtle, *Dermatemys mawei,* which occurs on the east coast of México as far north as Veracruz.

Specimens examined.—Total 275, as follows: ARIZONA: *Maricopa:* CNHM 4768, KU 2214-19, 2803, 2824, 2837, 2903-07, 2909-16 (2914, 2 specimens), 2918-29, 3118-27, 3129, 3147-56, USNM 71627, Salt River, Phoenix. *Pinal:* UI 37713, Gila River, 6 mi. E Winkleman; UMMZ 92006-07, Gila River, ½ mi.

below Coolidge Dam; UMMZ 105824, San Pedro River about 1 mi. above confluence with Gila River.

NEVADA: *Clark:* AMNH 58370, Boulder City boat landing, Lake Mead; TU 15802, Virgin River, Mesquite.

NEW MEXICO: *Eddy:* KU 15938, Carlsbad; KU 48217-18, Black River Village. *Grant:* AMNH 79911, Gila River, 8 mi. NE Cliff.

TEXAS: *Brewster*: CNHM 39999, Tornillo Creek near jct. with Río Grande; KU 51954-92, Lajitas; TCWC 4291, UMMZ 66471, USNM 45545, 103678, Boquillas; INHS 7975, UMMZ 114360, Hot Springs. *Cameron:* BCB 7564-73, CNHM 5339-40, 6810, MCZ 1909 (3), 1910, TU 11479-80, 11561-62, UMMZ 54021, 105209-13 (Brownsville Lake), USNM 7642, 7644, 7855, Brownsville; BCB 5121, 3 mi. S Harlington. *El Paso:* UMMZ 85085, El Paso; USNM 7641, 7701, El Paso del Norte. *Hudspeth:* USNM 20846, Fort Hancock on Río Grande. *Kinney:* CNHM 26090, Río Pinto W of Bracketville; USNM 26426-36, Fort Clark. *Loving:* TTC 1143, Red Bluff Lake just below dam on Pecos River. *Maverick:* TU 3696-97, UMMZ 116578, Eagle Pass. *Presidio:* TTC 628 (2), 632 (2), 3 mi. WNW Lajitas, Brewster County. *Terrell:* TNHC 7997, 8022-23, Chandler Ranch, 30 mi. S Sheffield, Pecos County; TNHC 8104, Dunlap Ranch, 25 mi. SE Sheffield, Pecos County; TU 14453 (7), 14462 (2), 15415, 15423, 15586, Pecos River near jct. with Independence Creek; USNM 104240, Pecos River "near" Dryden. *Val Verde:* TTC 113, Pecos River. *Webb:* TNHC 19788, 42 mi. NW Laredo; USNM 109078-79, Laredo. *Zapata:* UI 19332, "near" Zapata. *County unknown:* MCZ 1628, USNM 7635-36, 7854; USNM 7637-38, Río Bravo (= Río Grande).

CHIHUAHUA: KU 51173, 8 mi. S, 16 mi. W Ojinaga; KU 51174-86, 1 mi. NW Ojinaga; KU 51187-201, Río Conchos at mouth of Río San Pedro near Meoquí; UI 43508-09, Río Florida, La Cruz.

COAHUILA: CNHM 26054, Sta. Helena Canyon of Río Grande; CNHM 28846, "near" Músquis; CNHM 55657, Río Alamos, Rcho. de la Gacha; CNHM 47366, Sierra de Santa Rosa, La Palma; CNHM 47367, 55661, Cuatro Ciénegas; CNHM 55658-60, Rcho. de los Borregos near Juárez; KU 33523, La Presa Don Martín; KU 39991, 39993, 8 mi. N, 2 mi. W Piedras Negras; KU 39992, 2 mi. W Jiménez; KU 46907, 16 km. S Cuatro Ciénegas; KU 46913-16, 10 km. S Cuatro Ciénegas; KU 53752-54, Río Mesquites, 8 mi. W Nadadores; KU 53757, 8.5 mi. SW Cuatro Ciénegas; MSU 905-06, Río Sabinas, 1 mi. E Sabinas.

NUEVO LEON: CNHM 1874, 2191, Rodriguez; UMMZ 69411, Río Conchos, 9 mi. N Linares.

TAMAULIPAS: CM 3037, Nuevo Laredo. UMMZ 7614-20, 7622-25, 7628, 7630, 7632-33, Matamoros; UMMZ 69412, Río Purificación, N of Ciudad Victoria.

NO DATA: MCZ 1629 (2), NHB 1032.

Records in the literature.—ARIZONA: *Greenlee:* Gila River, Duncan (Miller, 1946:46); "near" Sheldon (Dill, 1944:180). *Mohave:* Pierce's Ferry just below lower end of Grand Canyon (Cowles and Bogert, 1936:42); 1.5 mi. upstream (Virgin River) from Mesquite, Clarke County, Nevada (Hardy and Lamoreaux, 1945:168); Lake Havasu on Colorado River (Dill, 1944:180). *Yuma:* Colorado River at Headgate Rock Dam (Dill, *op. cit.*:179).

CALIFORNIA: *Imperial:* California Lakes (Cowles and Bogert, 1936:42); Palo Verde; Colorado River at Laguna Dam (Dill, 1944:180).

NEVADA: *Clark:* observed just north of Black Canyon (Cowles and Bogert, *loc. cit.*); Colorado River, 6 mi. N California line (Linsdale, 1940:255).

NEW MEXICO: *Chaves:* Bitter Lakes Wildlife Refuge, 12 mi. NE Roswell (Bundy, 1951:314). *Dona Ana:* Río Grande near Mesilla Dam (Little and Keller, 1937:221).

TEXAS: *Brewster:* Río Grande at Castolon (Minton, 1959:38). *Val Verde:* mouth of Devil's River (Brown, 1950:250).

BAJA CALIFORNIA: Colorado River delta, 7 mi. E Cerro Prieto; Imperial

Irrigation District, Alamo Canal, 15 mi. S Internat'l Boundary and Salfatana Canal, 1 mi. N Black Butte (Linsdale and Gressitt, 1937:222).

COAHUILA: San Juan (Schmidt and Owens, 1944:103).

Hitherto, soft-shelled turtles of the species *Trionyx spinifer* from the southern and southwestern United States having a pattern of white dots on the carapace have been relegated to the subspecies *emoryi*, but my examination of soft-shelled turtles from Texas has indicated that *T. s. emoryi* as previously conceived, is a composite of three subspecies. It is necessary, therefore, to recognize two new subspecies.

Trionyx spinifer guadalupensis new subspecies

Guadalupe Spiny Softshell

Plates 41 and 42

Holotype.—UMMZ 89926, alcoholic adult male; obtained 15 miles northeast Tilden, McMullen County, Texas (Pl. 41, bottom, left).

Paratypes.—Forty-two specimens: ANSP 16717 (hatchling), no data; USNM 78515-16 (hatchlings), Colleto Creek, Victoria County, Texas; TU 10143-45, 10148, 10150-59, 10161-65 (adult males), TU 10176, 10833 (immature males), TU 10147, 10149, 10155 (immature females), TU 10160 (adult female), Guadalupe River, 9 miles southeast Kerrville, Kerr County, Texas; UMMZ 89915-21, 89924-27 (adult males), UMMZ 89922-23 (immature females), same locality as holotype; UMMZ 92752 (immature female), San Antonio River, 3 miles west-northwest Goliad, Victoria County, Texas.

Description of holotype.—Carapace nearly circular, widest at level of posterior border of hypoplastra; margin entire; dorsal surface "sandpapery" to touch; pale rim separated from ground color of carapace by well-defined, blackish line that is wavy and narrowly interrupted posteriorly and anteriorly; pale rim approximately 1.8 times wider posteriorly (5.4 mm.) than laterally (3.0 mm.); pale rim increasingly narrower anteriorly, absent in nuchal region; tubercles in nuchal region low, scarcely elevated, lacking sharp tips; ground color of carapace olive having pattern of whitish spots and small tubercles; most whitish tubercles inconspicuous pinpoints; other small tubercles in center of whitish spots, mostly approximately 2 millimeters in diameter; largest white spot 3.4 millimeters in diameter; most white spots surrounded by blackish ocelli or parts thereof; whitish spots distributed over entire surface of carapace; certain features of bony carapace evident through overlying skin; carapace highest in region of second and third neurals, forming obtuse, gently sloping, vertebral, keel; undersurface of carapace butterscotch yellow, lacking markings; maximum length, 16.5 centimeters; greatest width, 13.5 centimeters.

Plastral surface butterscotch yellow, lacking markings, extending slightly farther forward than carapace; anterior and posterior lobes rounded; anterior lobe slightly truncate; certain features of bony elements of plastron visible through overlying skin; maximum length of plastron, 12.0 centimeters.

Head, extended to posterior level of eyes, terminating in flexible snout; septal ridges projecting into each rounded nostril; jaws closed, each covered by fleshy lips except anteriorly where horny portions exposed; dark triangular mark in front of eyes, base line connecting anterior margins of orbits forming series of dots; pale stripes extending forward from eyes having faint inner, blackish borders; eyelids partly open having blackish dots; pale subocular blotch on right side of head having border of black dots.

Forefeet and hind feet well-webbed having five digits each; each limb having nails on first three digits; each forelimb with four antebrachial scales, three of these having free edge; each hind limb with two horny scales, one smooth on posterodorsal surface and other with free edge on posteroventral surface; pattern toward insertion of forelimbs indistinct.

Tail terminating in flexible point; penis exposed; cloacal opening extending beyond posterior edge of carapace; tail olive above bordered by blackish marks; few black dots laterally on left side.

Undersurface of soft parts of body buff, lacking markings; few dark marks posteriorly on webbing of limbs, encroaching on soles and palms.

Range.—South-central Texas in the drainage systems of the Nueces and Guadalupe-San Antonio rivers; the Colorado River drainage in Texas is inhabited by a population that more closely resembles *guadalupensis* than *pallidus*. See comments under subsection entitled "Remarks" and Fig. 19.

Diagnosis.—Juvenal pattern of white dots that are conspicuous on anterior half of carapace, and usually as large as those on posterior half; white dots, sometimes 3 millimeters in diameter, encircled with blackish ocelli in adult males.

Description.—Plastral length of smallest hatchling, 3.3 centimeters (ANSP 16717); of largest male, 13.5 centimeters (TU 10162); of largest female, 22.0 centimeters (TU 10160).

Hatchlings having white dots on anterior half of carapace; white dots anteriorly nearly as large as those posteriorly, encircled with blackish ocelli, and conspicuous on dark background (ANSP 16717, Pl. 41; USNM 78515-16; Stebbins, 1954:181, Pl. 26B), or smaller than those posteriorly, not encircled with dusky ocelli, and inconspicuous on pale background (TNHC 1446); pale rim of carapace less than four times as wide posteriorly as laterally.

Adult males resembling holotype; size of white tubercles on carapace variable; most, if not all, tubercles surrounded by narrow blackish ocelli, or parts thereof; largest white tubercles or dots in most specimens exceeding one millimeter and in some specimens three millimeters in diameter (TU 10163); white dots often slightly elongate (UMMZ 89917, 89920, 89926; TU 10152, 10145); juvenal pattern of white dots seemingly more contrasting in *guadalupensis*, owing to dark ground color of carapace, than in *pallidus* or *emoryi* that have pale brown or tan carapaces; small tubercles along anterior edge of carapace rounded, obtuse, wartlike, never conical; sharp tips often lacking (TU 10153).

Large females often having whitish spots on anterior half of carapace (TU 10160, Pl. 42, upper, right; 10142); carapace dark having ill-defined mottled and blotched pattern; tubercles along anterior edge of carapace low, rounded, rarely equilateral, never conical; small blackish dots rarely on surface of carapace (UMMZ 89923).

Pattern on side of head and snout of little diagnostic value; postocular stripe usually interrupted, but configuration variable, consisting of pale anterior, dark-bordered segment (just behind eye); posterior segment of postocular stripe usually less well-defined and generally blending with adjacent ground color; pale postocular stripe sometimes uninterrupted and dark-bordered throughout its length (TU 10157, 10159, 10176); pattern on dorsal surface of snout variable; pattern usually consisting of uninterrupted dark line (slightly curved anteriorly) connecting anterior margins of orbits (TU 10161, 10164, 10159, 10143), or dark line interrupted (TU 10153, 10154, 10176), absent (TU 10163), or present in addition to dark inner borders of pale stripes that extend anteriorly from eyes (TU 10149, 10162); small, often fine, dark markings, on dorsal surface of limbs, especially forelimbs; ventral surface of plastron and soft parts of body usually whitish, lacking markings; small blackish spots occasionally in region of bridge (TU 10149); dark marks occurring on webbing of limbs and often encroaching on soles and palms.

Ontogenetic variation in PL/HW, mean PL/HW of specimens having plastral lengths 7.0 centimeters or less, 3.83, and exceeding 7.0 centimeters, 5.18; ontogenetic variation in CL/CW, mean CL/CW of specimens having plastron lengths 8.5 centimeters or less, 1.14, and exceeding 8.5 centimeters, 1.22; mean CL/PCW, 2.11; mean HW/SL, 1.38 (including subspecies *pallidus*); mean CL/PL, 1.37.

Variation.—Two hatchlings (ANSP 13447, Bexar County; TNHC 1446, McMullen County) more closely resemble *pallidus* than *guadalupensis.*

Some individuals from the Colorado River drainage have features suggesting those that are characteristic of *pallidus.* Large females have obtuse, knoblike somewhat triangular-shaped tubercles along the anterior edge of the carapace, which are never conelike (TU 14439-40, 10187, 16036.1; BCB 6010). The tubercles along the anterior edge of the carapace are more elevated than in turtles from drainage systems west of the Colorado. Whitish spots are usually absent anteriorly on the carapace, but may be evident through the mottled pattern of large females (BCB 6010, plastral length, 19.7 cm.). The pale postocular stripe is usually interrupted, whereas the dark line connecting the anterior margins of the orbits is usually not interrupted; the two characters last mentioned show alliance with *guadalupensis.*

The carapace of hatchlings from the Colorado River is pale having whitish dots, smaller anteriorly than posteriorly, which may be encircled with dusky ocelli (TNHC 20257) or not (ANSP 11889, BCB 5055, SM 3282). Many hatchlings are not distinguishable from *pallidus* (TCWC 7262, TNHC 4975, SM 4924, 6106). I have not seen hatchlings from the Colorado River that resemble ANSP 16717.

The pattern on the carapace of adult males from the Colorado River drainage resembles that of *guadalupensis* (Pl. 41, bottom, right) but the whitish dots are usually smaller and may not be encircled with blackish ocelli (BCB 4066, TU 14485). An adult male (TU 14476) from the South Fork of the Llano River has whitish dots three millimeters in diameter and encircled with blackish ocelli (*guadalupensis*), whereas another adult male (USNM 83690) from a tributary of the Colorado, the South Concho River, resembles *pallidus.*

Eight specimens from the San Saba River (TU 14419 [6 specimens], 14439-40), that range in plastral length from 6.8 to 17.0 centimeters are impressive because of the dark brownish coloration on the carapace. The smallest individual, which is also the only male in the series, is paler. The mottled and blotched pattern on the females is therefore not contrasting; the largest females have elevated whitish prominences in the center of the carapace posteriorly. An immature male (UMMZ 70348) from the South Concho River also has a dark brown carapace, and lacks white dots. The dark coloration of the carapace of these specimens recalls the TU series of *T. s. emoryi* from the Pecos River, Terrell County, Texas.

Color notes taken from a freshly-killed adult female from the Llano River, two miles west Llano (TU 16036.1, Pl. 42), are: pattern on carapace of dark olive or blackish marks that form an irregular reticulum or marbling on a paler background that varies from brownish to buff and has an orange or reddish tinge in some areas; small whitish spots posteriorly; pale rim yellowish, evident only at sides of carapace; dorsal surface of soft parts of body olive-green, becoming paler with yellowish tinge toward insertions of limbs and neck; no contrasting pattern on limbs or neck and head; yellowish on sides of body; ventral surface whitish lacking dark marks, yellowish at region of bridge, axillary region and on neck; chin olive-yellow.

Comparisons.—*T. s. guadalupensis* can be distinguished from all other subspecies of *T. spinifer* in having: (1) large white dots, sometimes three millimeters in diameter, on a dark background usually surrounded with blackish ocelli and conspicuous on the anterior half of the carapace (some as large as those on posterior half) in adult males, and (2) whitish dots on the anterior half of the carapace, in hatchlings, that are often encircled with dark ocelli. *T. s. guadalupensis* resembles *pallidus* and *emoryi* in having white tubercles or dots on the carapace and therein differs from *spinifer, hartwegi* and *asper*. *T. s. guadalupensis* resembles *pallidus* but differs from *emoryi* in having a pale rim that is less than four times wider posteriorly than laterally. *T. s. guadalupensis* resembles *emoryi* but differs from *pallidus, spinifer, hartwegi* and *asper* in having along the anterior edge of the carapace tubercles that are flattened or wartlike prominences often lacking sharp tips in adult males; these tubercles are never conical in large females.

T. s. guadalupensis has a wide head, a feature shared with the subspecies *asper* and *emoryi,* but differs from *emoryi* in having a wider carapace. *T. s. guadalupensis* resembles *emoryi* and *pallidus* but differs from the other subspecies in having the carapace widest farther posterior than one-half the length of the carapace. The length of snout in *pallidus* and *guadalupensis* is shorter than in *spinifer* and *hartwegi* but is longer than in *emoryi*. *T. s. guadalupensis* differs from *asper* but resembles the other subspecies in having a relatively long plastron.

Remarks.—Some individuals of *guadalupensis* have characteristics that are applicable to *emoryi*. TNHC 12352 (Llano River) a hatchling, has conspicuous white dots confined to the posterior third of the carapace; the pale rim, however, is not widened posteriorly. TU 10156 (Guadalupe River) has a conspicuously widened pale rim on the carapace that is approximately 3.4 times wider posteriorly (8.5 mm.) than laterally (2.5 mm.).

T. s. guadalupensis more closely resembles *pallidus* than *emoryi*. Turtles living in rivers that drain into the Gulf of Mexico east of the Guadalupe-San Antonio river system successively show increasing resemblance to *pallidus* from west to east.

The expression of intergradation between *guadalupensis* and *pallidus* is of a clinal nature that involves parallel changes in the pattern on the snout, side of head, limbs (to a lesser degree), tuberculation along the anterior edge of the carapace, size of whitish tubercles or dots, and the distinctness of the blackish ocelli that surround the whitish dots on the carapace. These characters form a well-marked gradation or cline that extends over a considerable area. There is, however, no continuous environmental gradient because the populations are relatively isolated by occupying adjacent drainage systems. The sharpest break in the gradation of characters mentioned above occurs between the Colorado River and Brazos River drainages. The population of softshells in the Colorado River drainage is actually an intergradient one, but more closely resembles *guadalupensis*, whereas the population in the Brazos River drainage more closely resembles *pallidus*. For convenience the turtles inhabiting the Colorado River drainage are referred to *guadalupensis* and those in the Brazos River drainage to *pallidus*. Some individuals from farther west than the Colorado River drainage will resemble *pallidus*, and a few individuals from father east than the Brazos River drainage will resemble *guadalupensis*.

The gradation of some of the characters mentioned above terminates in the subspecies *emoryi*. It, however, has characters not found in *pallidus* or *guadalupensis*, and is more distinct from either of those subspecies than either is from each other; the difference in characters as well as the break in the gradient of characters between *guadalupensis* in the Nueces River drainage and *emoryi* in the Río Grande drainage is greater than that between *guadalupensis* in the Colorado and *pallidus* in the Brazos River drainages.

I have refrained from designating individuals between these three subspecies (*emoryi*, *guadalupensis* and *pallidus*) as "intergrades" on the distribution maps, and only mention (in text) those individuals whose characters show a decided tendency toward the adjacent subspecies. For further comments on intergradation see the account of *T. s. pallidus*.

Specimens examined.—Total 97, as follows: TEXAS: *Bandera:* KU 50834, Hondo Creek, 4 mi. W Bandera; TNHC 797-98, 7 mi. SW Medina. *Bexar:* ANSP 13447, Helotes; MCZ 4587; USNM 10789, 71009, San Antonio. *Borden:* BCB 4066, 7 mi. N Vincent. *Brown:* TNHC 7262, 1 mi. E Brownwood. *Comal:* USNM 7700, New Braunfels. *Dawson:* TNHC 21594-95, 10 mi. E Lamesa. *Frio:* USNM 7747, Río Seco. *Gillespie:* TU 10185, 10187, 10205, Beaver Creek, "near" Doss. *Hays:* AMNH 29950-52, San Marcos. *Kerr:* SM 2553, headwaters Turtle Creek; TU 10142-45, 10147-65, 10176, 10833, Guadalupe River, 9 mi. SE Kerrville. *Kimble:* BCB 5052-55, 6010, 3 mi. SE Telegraph; TU 14476, South Fork Llano River, 1.5 mi. SE Telegraph; TU 14485, Llano River, 10 mi. W Junction. *Lavaca:* SM 2554-55, 2559, 3 mi. NNE Hope. *Llano:* TNHC 12352, TU 16036 (2), Llano River, 2 mi. W Llano. *McMullen:* TNHC 1446, 10 mi. W Simmons, Live Oak County; UMMZ 89915-27, 15 mi. NE Tilden. *Matagorda:* ANSP 11889, Matagorda. *San Saba:* SM 6106; TU 14419 (6), 14439-40, San Saba River, 11 mi. NNW San Saba. *Tom Green:* SM 3282, UMMZ 70348, USNM 83690, South Concho River at Christoval. *Travis:* SM 659-60, 8.5 mi. from mouth of Onion Creek in Colorado River near Austin; SM 4924, Onion Creek; TNHC 4975, Upper Bull Creek; TNHC 20257, Marshall Ford Dam. *Victoria:* CM 3118, Black Bayou; UMMZ 92752, San Antonio River, 3 mi. WSW Goliad; USNM 78515-17, Colleto Creek, Guadalupe River. *County unknown:* ANSP 16717; TNHC 1404.

Records in the literature.—TEXAS: *Bandera:* 24 mi. WNW Medina (Brown, 1950:250). *Burnet:* Colorado River (Strecker, 1909:8). *Gillespie:* 20 mi. N Harper (Brown, *loc. cit.*). *Kendall:* Cibolo Creek at Boerne (Strecker, 1926:8). *Kerr:* Guadalupe River, 3 mi. above Kerrville (TCWC 474, listed in card file). *Mason:* 12 mi. NE Mason (TCWC 3303, listed in card file).

Matagorda: Bay City (Brown, *loc. cit.*). *Real:* (Stejneger, 1944:66). *Wilson:* Cibolo River, 30 or 40 mi. N Sutherland Springs (Strecker, 1935:23).

Trionyx spinifer pallidus new subspecies

Pallid Spiny Softshell

Plates 39 and 40

Holotype.—TU 484, alcoholic adult male; obtained from Lake Caddo, Caddo Parish, Louisiana on June 27, 1947, by Fred R. Cagle and party (Pl. 39, lower, left).

Paratypes.—Forty-two specimens: TU 481, 490, 678 (hatchlings), TU 381, 472, 488 (immature males), TU 475, 478, 486, 1232, 1291, 10170 (adult males), TU 399, 487 (immature females), TU 469 (adult female), Caddo Lake, Caddo Parish, Louisiana; TU 15818 (immature male), TU 15819 (adult male), Cross Lake, Caddo Parish, Louisiana; TU 1253, 13211 (adult males), TU 13266 (immature female), Sabine River, 8 miles southwest Merryville, Beauregard Parish, Louisiana; TU 13281-82 (adult males), TU 13280, 13265 (immature females), TU 13303-04, 13306 (adult females), Sabine River, 8 miles southwest Negreet, Sabine Parish, Louisiana; SM 2375 (adult male), Wallace Bayou, De Soto Parish, Louisiana; TU 1122 (adult male), Lacassine Refuge, Louisiana; UMMZ 92754 (adult male), 5 miles west Iowa, Calcasieu Parish, Louisiana; KU 40174-76, OU 27297 (adult males), OU 27290 (immature female), Lake Texoma, 2 mi. E Willis, Marshall County, Oklahoma; KU 50832 (hatchling), mouth of Caney Creek, 4 miles southwest Kingston, Marshall County, Oklahoma; CNHM 15474 (immature female), Kiowa County, Oklahoma; KU 2966-67 (immature females), KU 2934, 2947 (adult males), KU 2973 (adult female) Lewisville, Lafayette County, Arkansas.

Description of holotype.—Carapace circular, widest at level of posterior edge of hyoplastra; margin entire; dorsal surface "sandpapery" to touch; pale rim separated from ground color of carapace by well-defined, slightly ragged, blackish line; pale rim approximately 2.1 times wider posteriorly (4.7 mm.) than it is laterally (2.2 mm.); pale rim increasingly narrower anteriorly, absent in nuchal region; tubercles along anterior edge of carapace triangular with sharp tips becoming flattened and inconspicuous at level of insertions of arms; ground color of carapace brownish having pattern of small whitish tubercles; most whitish tubercles inconspicuous, of pinpoint size, giving surface of carapace "sandpapery" effect; largest white tubercles posteriorly, approximately 1.2 millimeters in diameter; whitish tubercles smaller anteriorly, largest approximately 0.6 millimeters in diameter; whitish tubercles tend to form two parallel lines coincident with longitudinal sutures of neurals posteriorly in center of carapace; certain features of bony carapace evident through overlying skin; carapace highest in region of third and fourth neurals, forming obtuse, gently sloping, vertebral keel; undersurface of rear margin of carapace whitish having pinkish tinge and no markings; maximum length, 16.8 centimeters; greatest width, 14.3 centimeters.

Plastral surface extending slightly farther forward than carapace, whitish having pinkish tinge and no dark markings; anterior and posterior lobes rounded, posterior lobe more acutely; certain features of bony elements of plastron visible through overlying skin; maximum length, 12.2 centimeters.

Head extended, terminating in flexible snout; septal ridges projecting into each rounded nostril; tip of snout darkened; jaws open, each covered by fleshy lips except anteriorly where horny portions exposed; dark triangular mark in front of eyes, base line uninterrupted, slightly curved anteriorly, connecting anterior margins of orbits; eyelids having blackish dots, especially upper, closing eyes; small blackish dots on dorsal surface of head; pale postocular stripe dark-bordered, interrupted; pale portion of stripe traversed by black line; pale subocular blotch margined by broken blackish border; side of head having contrasting blackish marks on pale background; postlabial stripe having lower blackish border on right side of head; chin with ill-defined marks, not contrasting on grayish background; well-defined, ragged black line on side of neck separating dorsal coloration from immaculate ventral coloration; small dark dots on dorsal surface of neck; dorsal surface of head and neck olive or brownish, becoming paler laterally and toward insertion of neck; maximum width of head, 2.1 centimeters.

Forefeet and hind feet well-webbed each having five digits; each limb having nails on first three digits; each forelimb with four antebrachial scales, three of which have free edge; each hind limb with two horny scales, one smooth on posterodorsal surface and other with free edge on posteroventral surface; contrasting pattern of blackish marks, mostly roundish, on pale background of grayish-white.

Tail terminating in flexible point; penis partly exposed; cloacal opening extending beyond posterior edge of carapace; tail having dorsal grayish band flanked by interrupted blackish lines; dark marks encroaching ventrally at tip of tail.

Undersurface of soft parts of body whitish, with pinkish tinge; dark marks lacking on soles, present on webbing and palms; dark marks arranged in linear fashion coincident with digits.

Range.—Southern Oklahoma, eastern Texas, extreme southwestern Arkansas, and the western half of Louisiana; Red River drainage and rivers that drain into the Gulf of Mexico east of the Brazos River drainage in Texas and west of the Atchafalaya River drainage in Louisiana. The Brazos River drainage is inhabited by a population that more closely resembles *pallidus* than *guadalupensis* (see comments under subsection entitled "Remarks"; see map, Fig. 19).

Diagnosis.—Juvenal pattern of white dots that are usually absent or inconspicuous, but sometimes distinct and small, on anterior third of carapace, and not surrounded with dark ocelli; white dots often absent on posterior half of carapace of hatchlings; white spots, rarely as large as two millimeters in diameter, not encircled with black ocelli on adult males; pale rim of carapace less than four times wider posteriorly than laterally.

Description.—Plastral length of smallest hatchling, 3.3 centimeters (KU 50832); of largest male, 16.0 centimeters (SM 2375); of largest female, 30.5 centimeters (TU 13213).

Surface of carapace in hatchlings uniform pale brown or tan; small white tubercles absent or inconspicuous on anterior half of carapace, but evident on posterior half of carapace, sometimes well-defined (TU 481), but usually inconspicuous (TU 678, 490); pale rim of carapace less than four times wider posteriorly than laterally.

Adult males resembling description of holotype; small whitish tubercles or dots rarely two millimeters in diameter on posterior half of carapace, smaller and usually inconspicuous on anterior half of carapace (TU 13281, 486); well-defined whitish tubercles occasionally on anterior half of carapace (KU 40174); white tubercles not surrounded with black ocelli; pattern of white dots seemingly less contrasting in *pallidus* than in *guadalupensis,* owing to pale brown or tan carapace; small tubercles along anterior edge of carapace equilateral or conical having sharp tips.

Large females usually having pale brown carapaces with slightly contrasting, brownish, mottled and blotched, patterns; white prominences often evident posteriorly and anteriorly in middle of carapace and in nuchal region; tubercles along anterior edge of carapace equilateral or conical in shape.

Pattern on side of head and snout variable and of no diagnostic value; postocular stripe uninterrupted having dark borders (UMMZ 92754), or interrupted having pale segment behind eye (TU 13282); other variations in pattern shown on TU 10170 and 15818; pale stripes on snout having dark inner borders that join and form acute angle (TU 381), or lacking dark inner borders and having uninterrupted dark line connecting anterior margins of orbits (TU 13280); other variations in pattern on snout shown on TU 1232, 1291 and 15819; specimens representing illustrations of variation in pattern on snout (Fig. 5 d, e, f) all from same locality, Lewisville, Lafayette County, Arkansas; contrasting pattern on side of head of dark marks on pale background; contrasting pattern of dark marks on dorsal surface of limbs; markings on hind limbs generally larger than those on forelimbs; small or fine markings ot some specimens reducing contrast in pattern (TU 478, 488); carapace sometimes having few small blackish dots confined to margin (CNHM 15474, TU 487, 1253, 13266); ventral surface of plastron and soft parts of body whitish and usually lacking dark markings; small blackish marks often occurring on flap of carapace, in region of bridge, or on chin and throat (TU 399, 469, 475, 472, 13281).

Ontogenetic variation in PL/HW, mean PL/HW of specimens having plastral lengths 7.0 centimeters or less, 4.15, and exceeding 7.0 centimeters, 5.32; ontogenetic variation in CL/CW, mean CL/CW of specimens having plastral lengths 8.5 centimeters or less, 1.10, and exceeding 8.5 centimeters, 1.14; mean CL/PCW, 2.12; mean HW/SL, 1.38 (including subspecies *guadalupensis*); mean CL/PL, 1.36.

Variation.—In 1953, I casually glanced at a hatchling softshell from the Calcasieu River drainage in the private collection of Mr. Wilfred T. Neill; the specimen was considered by Neill (1951:15) as ". . . an intergradient one (with the *hartwegi-spinifer* population in the lower Mississippi drainage)." The hatchling does deviate from "typical" *pallidus* in having darkish flecks posteriorly on the carapace.

I have seen only one adult male (USNM 94457) from the Sabine River drainage (Orange County, Texas) that shows characteristics of *guadalupensis* (white dots on carapace encircled with small black ocelli); another adult male (USNM 94456) from the same locality resembles *pallidus*. Those two USNM specimens were mentioned by Neill (1951:13) as indicating intergradation with ". . . the mixed *spinifera-hartwegi-asper* populations of Louisiana."

Two adult males (SM 2889, Pl. 40, bottom, left, and TCWC 471, Trinity River drainage) have blackish ocelli surrounding the white dots on the posterior part of the carapace; two large females (TU 14402, Pl. 40, bottom, right, plastral length, 17.5 cm., and TU 14417 plastral length, 21.3 cm., both from the Trinity River) have contrasting mottled and blotched patterns with white dots visible on the carapace. These turtles show alliance with *guadalupensis.*

Some individuals from the Brazos River drainage have features suggesting those that are characteristic of *guadalupensis.* Hatchlings may have large white dots on the anterior half of the carapace (USNM 55601). Adult males may have dusky ocelli surrounding the white dots on the carapace (TU 14169, 14559.1, 14559.2). The whitish dots, rarely as large as two millimeters, are never so large as in *guadalupensis* (three mm. in diameter), and are usually smaller anteriorly than posteriorly; TU 14169 has white dots approximately the same size (1.2 mm.) on the anterior half as on the posterior half of the carapace. The tubercles on adult males are equilateral or subconical, usually having sharp tips (TU 14348, 14559.1, 14559.2); the tubercles on large females are subconical, resembling the end of a bullet, and, in both sexes the tubercles are less conical than those on specimens of *pallidus* from farther east.

Three specimens from the Brazos River drainage are particularly impressive in their alliance with *guadalupensis.* SM 2556, an adult male, has large white dots that are encircled with black ocelli on the posterior half of the carapace, but lacks white dots on the anterior half. TNHC 14068, a hatchling, has small black dots interspersed with the larger white dots posteriorly. CNHM 46289 has large white spots on the carapace that are surrounded with two to four black dots; scattered black dots also intermix with white spots on the surface of the carapace (less extensive anteriorly).

Color notes taken from a freshly-killed adult male (KU 47121) from the Brazos River, seven miles below Whitney Dam, Bosque-Hill county line, Texas, are: Carapace pale brown or tan bordered by black line, having pale lemon yellow rim; yellowish-cream spots on carapace faintly surrounded with black stippling; dorsal surface of soft parts of body olive having black marks and patches of grayish; webbing on limbs having golden or yellowish hue, brighter distally; interorbital region brown; black-bordered, postocular stripe orange-cream; snout and side of head olive having pale areas of orange-cream; iris cream having black stripe; yellowish at juncture of dark dorsal and pale ventral coloration with orangish tinge on forelimbs and head; tail pale brown or tan, flanked by black borders that suffuse laterally into lemon-yellow; undersurface whitish, pale yellow on neck, bluish-gray on throat.

Comparisons.—T. s. pallidus most closely resembles *T. s. guadalupensis,* but can be distinguished from that subspecies in having small white tubercles, rarely two millimeters in diameter, on a pale background, that are not surrounded by blackish ocelli, and are usually absent, or not conspicuous on the anterior third of the carapace in adult males; also there are usually no conspicuous white tubercles or dots on the anterior third of the carapace in hatchlings. Many adult males of *pallidus* from the Brazos and some from the Trinity River drainages often have dusky or black ocelli surrounding the white dots posteriorly on the carapace; males from these river systems may be distinguished from *guadalupensis* in having most, if not all, white dots on the anterior half of the carapace smaller than those posteriorly, and a pale brown carapace (in life, usually darker in *guadalupensis*). *T. s. pallidus* (and *guadalupensis*) is distinguished from *emoryi* in lacking a widened pale rim posteriorly, and in having small white spots on the anterior half of the carapace. *T. s. pallidus* resembles *guadalupensis* and *emoryi* in having white spots on the carapace in adult males. *T. s. pallidus* differs from *spinifer, hartwegi* and *asper* in lacking blackish dots or ocelli that occur in the center of the carapace. *T. s. pallidus* resembles *emoryi* but differs from *guadalupensis* in lacking black ocelli surrounding the white spots. *T. s. pallidus* resembles *spinifer, hartwegi* and *asper* but differs from *guadalupensis* and *emoryi* in having tubercles along the anterior edge of the carapace that are conical having sharp tips in males, and conical in large females.

T. s. pallidus resembles *spinifer* and *hartwegi* but differs from the other subspecies in having a narrow head. *T. s. pallidus* differs from *emoryi* but resembles the other subspecies in having a wider carapace. *T. s. pallidus* resembles *emoryi* and *guadalupensis,* and differs from the other subspecies in having the carapace widest farther posterior than one-half the length of the carapace. The snout of *pallidus* and *guadalupensis* is shorter than in *spinifer* and *hartwegi,* but longer than in *emoryi. T. s. pallidus* differs from *asper* but resembles the other subspecies in having a relatively long plastron.

Remarks.—Intergradation of the subspecies *pallidus* and *guadalupensis* is of a clinal nature in which populations successively show a gradual resemblance to *guadalupensis* from western Louisiana and eastern Texas westward to central Texas. Because the sharpest break in this cline of characters occurs between the Colorado and Brazos River drainages, the turtles living in the Brazos River drainage and eastward are referred to *pallidus,* whereas those in the Colorado River drainage and westward are referred to *guadalupensis.* For further comments on intergradation between these two subspecies, see the account of *T. s. guadalupensis.*

Taylor (1935:217-18) reported on some specimens of *Amyda spinifera* that were obtained by Mr. R. E. McEntyre in ". . . the spring and summer of 1926, chiefly about Lewisville, Lafayette County (Arkansas)." Of the catalog numbers listed by Taylor from Lewisville, 58 (KU, alcoholic) represent *pallidus.* Three, having the same locality data, have features that are characteristic of *hartwegi.* KU 2944 (one of three specimens having this catalog number) is a female having a pale, mottled and blotched carapace approximately one foot in length; there are remnants of two dark ocelli, and many widely-scattered, well-defined dark spots near the periphery of the carapace. KU 2963 (one of three specimens having this catalog number) is an adult male that has solid, blackish dots on the entire surface of the carapace. KU 2964 (one of two specimens with this catalog number) is an adult male that has ocelli approximately five millimeters in diameter on the carapace (indistinct in center of carapace).

Lewisville is situated in the drainage basin of the Red River and is approximately eight miles east of the Red River and 30 miles west of the westernmost tributary of the Ouachita River drainage. *T. s. pallidus* occurs in the Red River drainage; *hartwegi* occurs in the Ouachita River drainage. Perhaps there is intergradation between *pallidus* and *hartwegi* in the intervening streams. There is no data to indicate from which river or stream each specimen obtained by McEntyre came; one would presume that all specimens came from the Red River drainage. But this is not certain. Certainly the 47 specimens designated herein as *pallidus* came from the Red River drainage. I suspect that KU 2944, 2963 and 2964 were obtained from tributaries of the Ouachita River drainage.

T. s. pallidus intergrades with the *spinifer-hartwegi* population where the Red River joins the Mississippi River in the lower Mississippi Valley in Louisiana. The majority of 13 juvenal specimens from the Red River near Shaw, Concordia Parish, Louisiana (USNM 99862-69, 99871-75), resemble *pallidus* in having inconspicuous white tubercles on a pale brown carapace. The white tubercles are conspicuous in USNM 99871. Some specimens have a few small dark dots confined to the margin of the carapace, as do some "variant" individuals from well within the geographic range of *pallidus.* USNM 99865 is referred to *hartwegi* because the carapace is covered with dark ocelli approximately one millimeter in diameter. Some specimens from farther west in the Red River drainage are referred to *hartwegi.* One (USNM 100420) of three from Natchitoches Parish, Louisiana (TU 5763, USNM 100420-21), having blackish dots on the carapace, is applicable to *hartwegi.* Of two turtles from Grant Parish, Louisiana (TU 5647, 12735), only 12735 has dark dots and ocelli (*hartwegi*). One specimen from Rapides Parish, Louisiana (TU 14040), having dark dots on the entire surface of the carapace, is referred to *hartwegi.*

Most specimens from the lower Atchafalaya River drainage are referable to *pallidus.* Eastward, intergradation occurs with the *spinifer-hartwegi* population; USNM 100089-90 from Assumption Parish, near Napoleonville, Louisiana, are referred to *pallidus.* TU 11983, from Bayou Lafourche, Raceland, La Fourche Parish, and TU 13698.11, from Bayou Gauche in St. Charles Parish, Louisiana, are juvenal males that combine the characteristics of *pallidus* and *hartwegi*; the carapaces are covered with blackish spots and posteriorly have distinct whitish dots. The population in the Atchafalaya River more closely resembles *pallidus* than it does *hartwegi* or *spinifer.* In former times the Atchafalaya River was presumably continuous solely with the Red River (inhabited by *pallidus*). Now, these two rivers and the Mississippi River are interconnected in east-central Louisiana. A large volume of water of the Mississippi drainage is conveyed to the Gulf of Mexico by the Atchafalaya, and someone has said that by approximately 1975, unless man interferes, two-thirds to three-fourths of the total volume of water of the Mississippi River will be drained by the Atchafalaya. One can expect, therefore, an increase in the influence of the *hartwegi-spinifer* population in the Atchafalaya River drainage.

Specimens examined.—Total 270, as follows: ARKANSAS: *Lafayette:* KU 2930-37, 2939-40, 2942, 2944 (two of three specimens bear this catalog number), 2945-57, 2958 (2), 2959-61, 2963 (two of three specimens bear this catalog number), 2964 (one of two specimens bears this catalog number), 2965-73, 2987-89, 3056, Lewisville.

LOUISIANA: *Acadia:* USNM 100151-59, Mermentau River. *Assumption:* USNM 100089-90, Bayou Lafourche, "near" Napoleonville. *Beauregard:* TU 1231-32, 1253-55, 1291, 13211, 13266, Sabine River, 8 mi. SW Merryville. *Bienville:* TU 5649-50, Lake Bistineau. *Caddo:* TU 381, 397-99, 469-72, 474-90, 678, 10170, Caddo Lake: TU 15818-19, Cross Lake. *Calcasieu:* UMMZ 92754, 5 mi. W Iowa. *Cameron:* TU 1122, Lacassine Wildlife Refuge. *Concordia:* USNM 99862-64, 99866-69, 99871-75, Red River, "near" Shaw. *De Soto:* SM 2374-75, Wallace Bayou. *Grant:* TU 5647, Lake Iatt. *Iberville:* USNM 83985, 2 mi. E Mounds; USNM 100239-41, Grand Lake west of White Castle; USNM 100380, Plaquemine; USNM 100412, 100414-15, 100419, Spanish Lake, "near" St. Gabriel. *Jefferson Davis:* Calcasieu River drainage, WTN (no number, see page 524). *Natchitoches:* TU 5763, Bermuda; USNM 100421, "near" Natchitoches. *Sabine:* TU 13210, 13212-13, 13265, 13280-82, 13303-06, Sabine River, 8 mi. SW Negreet. *St. Martin:* USNM 100160, Bayou Chene; USNM 100650, Atchafalaya. *St. Mary:* USNM 100395-97, 100404, 100409-10, Berwick Bay near Morgan City.

OKLAHOMA: *Atoka:* OU 8966, Rock Creek, 10 mi. E Atoka; OU 8978, McGee Creek, 7 mi. SW Daisy. *Caddo:* ANSP 100, Washita River, Fort Cobb.

Choctaw: OU 27126, Mayhew Creek, 2 mi. NW Boswell. *Comanche:* OU 4130, 4266, 5390, 8333, 12953, 19986, Wichita Mountains Wildlife Refuge. *Jackson:* OU 13012, 6 mi. E El Dorado. *Kiowa:* CNHM 15474. *Le Flore:* OU 6791, Kiamichi River, 8 mi. W Arkansas State Line. *McCurtain:* OU 2149-50, 2152, 2155, 17126-28, 17185, 2 mi. SW Smithville; USNM 70397, Red River. *Marshall:* KU 40175-76, 50830-31, 50847, OU 27290, 27297, 27562-63, TU 16076 (5), 16175 (6), 16662 (5), Lake Texoma, 2 mi. E Willis; KU 50832, mouth of Caney Creek, 4 mi. SW Kingston. *Pushmataha:* OU 2151, 2157; OU 11365, Buffalo Creek, 5 mi. NW Tuskahoma.

TEXAS: *Archer:* TU 16174, 16668-69, Lake Diversion. *Bell:* SM 5667-69, Nolan Creek. *Bosque:* KU 47121, 7 mi. below Whitney Dam, Brazos River. *Brazos:* BCB 4436, 10 mi. E College Station; BCB 4437, 17 mi. S College Station; BCB 4438, 4 mi. N Bryan; KU 50833, 4 mi. W College Station; SM 2556, TCWC 472, Wickson Lake; TCWC 539, Little Brazos River; TCWC 4692, 8 mi. NE Bryan; TCWC 5121, 2 mi. S College Station; TCWC no number. *Clay:* TCWC 7258, 8 mi. NW Ringgold, Montague County; TU 16667.1, 3 mi. W Byers. *Dallas:* MCZ 3987, "near" Dallas; ANSP 13243, Dallas. *Donley:* ANSP 13440, S of Clarendon. *Eastland:* KU 3132, Cisco. *Galveston:* TCWC 7251, Alta Loma. *Harris:* UMMZ 92753, Little Cypress Creek, 1 mi. N Westfield; USNM 94335-36, "near" Houston. *Harrison:* USNM 95386, 16.5 mi. SE Caddo Lake. *Hill:* TU 14169, Richland Creek, 0.7 mi. W Mertens. *Leon:* CNHM 46290, 5 mi. W Marquez; TCWC 8994, 8996, 6 mi. NW Normangee. *Liberty:* TU 14402, 14417, Trinity River, "near" jct. with Big Creek. *McLennan:* BCB 4665-66, 6 mi. NNE McGregor; SM no number, 2037, 2452, 2552, 2558, 2560, 2640, 5263, 6533, Lake Waco; SM 0185, Middle Bosque River; SM 2104, 6732, Upper Bosque River; SM 5072, Bull Hide Creek; UI 2399, 1.5 mi. W China Springs; UMMZ 64063, Waco; USNM 55601. *Madison:* TCWC 471, 517, Twin Lakes. *Montgomery:* TCWC 540, 3 mi. S Conroe. *Nacogdoches:* TNHC 14112, Legg Creek, 5 mi. S Douglass. *Orange:* UMMZ 117060, 3 mi. S Orange; USNM 94456-57, Orange. *Randall:* TTC 576, Palo Duro Canyon, 15 mi. SE Canyon. *Shackelford:* TU 14547, Clear Fork Brazos River, Fort Griffin State Park. *Somervell:* TCWC 8995, TU 14559 (4), Brazos River, 5-6 mi. E Glen Rose. *Trinity:* SM 2889, Groveton. *Walker:* TNHC 20829, 5 mi. E New Waverly. *Waller:* TNHC 14068, 2.7 mi. E Brazos River on US 90. *Williamson:* MCZ 1627 (2); TU 14348, San Gabriel River, 6.5 mi. E Georgetown. *County unknown:* ANSP 13448, Wichita River; USNM 7640, Brazos River.

Records in the literature.—LOUISIANA: *Cameron:* Sabine Refuge (Cagle and Chaney, 1950:386).

OKLAHOMA: *Le Flore:* 6 mi. W Page. *McCurtain:* 14 mi. SE Broken Bow (Trowbridge, 1937:301).

TEXAS: *Bosque:* Bosque River, "near" Valley Mills (Strecker, 1928:6). *Harris:* Addicks (Brown, 1950:250). *Henderson:* Cedar Creek (Strecker, 1926a:7). *Jefferson:* 12 mi. SW Port Arthur (Guidry, 1953:56). *Liberty:* Daisetta (Brown, *loc. cit.*); San Jacinto River (Strecker, 1915:15). *McLennan*: "near" Crawford (Brown, *loc. cit.*). *Orange:* 1 mi. N Bridge City (Guidry, *loc. cit.*). *Tarrant:* Trinity River, Fort Worth (Stejneger, 1944:66). *Taylor:* Abilene (KKA). *Tyler:* Colmisneil (Siebenrock, 1909:603). *Walker:* 6 mi. E Huntsville (TCWC 329, listed in card file). *Wheeler:* 5 mi. N Wheeler (Brown, *loc. cit.*).

Trionyx ater Webb and Legler

Black Softshell

Trionyx ater Webb and Legler, Univ. Kansas Sci. Bull., 40:21, pls. 1 and 2, 1960, April 20.

Type.—Holotype, KU 46903, alcoholic female; obtained 16 km. S Cuatro Ciénegas, Coahuila, México, by John M. Legler (and party), September 6, 1958.

Range.—Basin of Cuatro Ciénegas, central Coahuila, Mexico (see map, Fig. 22).

Diagnosis.—Posterior margin of carapace of some females having fine corrugations, edge often ragged, and no pale outer margin; septal ridges reduced in adult males; over-all dorsal coloration (in preservative) dark, lacking contrasting patterns.

Description.—Plastral length of adult male, 9.6 centimeters (KU 46911); of largest female, 18.4 centimeters (KU 46903).

Adult male: anterior edge of carapace smooth; septal ridges reduced; pale outer rim, and small, whitish, dots posteriorly on carapace; surface of carapace slightly gritty or sandpapery posteriorly; snout broadened; over-all dorsal coloration dark gray or slate; contrasting pattern on soft parts of body lacking; ventral surface whitish having few blackish marks posteriorly on undersurface of carapace.

Females: posterior margin of carapace usually having fine corrugations; edge of carapace posteriorly often ragged; pale rim of carapace absent; mottled and blotched pattern not contrasting on blackish carapace; dorsal surface of soft parts of body dark gray or slate, lacking contrasting pattern; ventral surface of carapace and posterior part of plastron usually having many blackish flecks and markings; tubercles lacking on anterior edge and in center of carapace posteriorly; septal ridges well developed.

Medial angle of epiplastron (as observed through overlying skin) bent at angle of approximately 90 degrees. Other osteological characters presumably as in *spinifer*.

Range in length of plastron (cm.) of 11 females (mean follows extremes); 10.8-18.4, 15.0; proportional measurements of 12 specimens (including adult male, mean follows extremes): PL/HW, 4.70-5.43, 4.93; CL/CW, 1.28-1.43, 1.32; CL/PCW, 1.98-2.42, 2.15; HW/SL, 1.22-1.58, 1.37; CL/PL, 1.29-1.44, 1.36; some females (especially KU 46908) have noticeably elongate carapaces.

Variation.—Corrugations best-developed on two largest females (KU 46903, 46906), even present on ventral surface of carapace posteriorly and on dorsal surface of tail; development of corrugations not ontogenetic phenomenon as posterior margin relatively smooth on KU 46908 (plastral length, 16.0 cm.) but relatively rugose on KU 46909, which is smaller (plastral length, 13.9 cm.); smallest female (KU 46904) and adult male having posterior margin smooth; smallest female having indication of pale outer rim and small whitish dots posteriorly on carapace, and dark, obtusely-angular line, connecting anterior margins of orbits; blackish marks on ventral surface reduced on KU 46904, 46910, 46912, and UI 43510; UI 43510 (plastral length, 16.3 cm.) resembles *T. s. emoryi* in having more contrasting mottled pattern on carapace and limbs, indication of pale outer rim on carapace, and dark line connecting anterior margins of orbits; ventral surface of tail and hind limbs often tinged with red.

Color notes from life of young female, topotype (KU 53755) are: mottled carapace dark brown, pale areas buff; dorsal surface of head mottled, olive-brown, pale areas buff; iris orange-buff; upper and lower lips yellow-orange; dorsal surface of limbs olive-brown having yellow to buff suffusion and small blackish marks; pale areas on webbing yellow; ventral surface whitish having yellow at margin of carapace, on neck and limbs.

Comparisons.—*T. ater* most closely resembles *T. spinifer* (especially the subspecies *emoryi*) in having a gritty or "sandpapery" carapace (reduced, tubercles more scattered), whitish dots on posterior third of carapace (small females and adult male) and a dark line connecting anterior margins of orbits (smallest female). Prior to acquiring the characteristic darkened, dorsal ground color, the pattern on the head and limbs seems to be that of *T. s. emoryi.*

T. ater resembles *T. muticus* in having reduced septal ridges in males, a smooth anterior edge of carapace (especially males), and no enlarged prominences on the anterior edge of the carapace or posteriorly in the center of the carapace on large females. *T. ater* resembles *T. ferox* in having an over-all dark coloration dorsally with no contrasting patterns on adults.

T. ater probably is a small species resembling *T. muticus* and *T. spinifer emoryi.* The head is wide in *T. ater,* resembling that of *T. ferox,* and closely approaching that of *T. spinifer emoryi* and *T. s. guadalupensis. T. ater* resembles *T. ferox* and *T. s. emoryi* in having a narrow carapace. *T. ater* resembles *T. s. emoryi, T. s. guadalupensis* and *T. s. pallidus,* but differs from *T. muticus, T. ferox* and the other subspecies of *T. spinifer* in having the carapace widest farther posterior than one-half the length of the carapace. *T. ater* resembles *T. ferox* and *T. s. emoryi* in shortness of snout. The plastron is short in *T. ater* and most closely resembles that of *T. s. pallidus, T. s. guadalupensis,* and *T. s. emoryi.*

Remarks.—*T. ater* is confined to permanent, clear-water ponds in the basin of Cuatro Ciénegas. The male and 11 females (KU) were taken at the type locality (a pond known locally as Tío Candido); the other female (UI 43510) was taken from a pond approximately seven miles northward (known locally as Anteojo). *T. spinifer emoryi* also occurs in the basin of Cuatro Ciénegas. Males and females of *emoryi* were collected in the Río Mesquites (Río Salado drainage) that drains the basin; two adult males of *emoryi* were taken from the clear-water ponds—one from the type locality of *ater* (KU 46907), and the other (KU 53757) from a pond (known locally as El Mojarral) from which no *ater* were obtained. This demonstrated sympatry indicates that the two kinds are not conspecific.

However, the nature and frequency of occurrence of characters of *T. ater,* suggest that it is subspecifically related to *T. spinifer*—in effect, a darkened race of *T. s. emoryi.* The diagnostic characters of fine corrugations on the posterior margin of the carapace and blackish marks on the ventral surface do not occur on every female of *ater.* Too, the dorsal coloration of living females (dark brown-buff) is paler than that of preserved specimens (dark gray-slate). Furthermore, a hatchling (CNHM 47367) recorded from Cuatro Ciénegas, Anteojo, is not distinguishable from *emoryi.*

The mention of absence of septal ridges in males of *T. ater* in the original description (Webb and Legler, 1960:22) should be amended. The septal ridges in the only known adult male are reduced; a small, whitish ridge is present on the medial surface of each nostril, but is not conspicuous in anterior view. The one adult male of *ater* is distinguished from *T. s. emoryi* principally on the over-all dark, dorsal coloration with concomitant loss of pattern, the noticeably broadened snout, and the reduced septal ridges. The last character mentioned possibly is variable in *ater* (and in *emoryi* in this region) in view of the variation in development of the ridge on four male *emoryi* from the basin: well-developed on KU 53757 (Mojarral) and KU 46907 (Tío Candido); reduced on KU 53752 (Río Mesquites), resembling development in *ater;* and, reduced on right side only on KU 53753 (Río Mesquites).

Presumably, the continued erosive action at the headwaters of the Río Salado has permitted the invasion of this drainage into the formerly isolated basin of Cuatro Ciénegas. In the basin, however, I know of no evidence of a direct aquatic contact between the headwater streams and the isolated, clear-water, ponds. How *emoryi* entered the ponds is unknown. Some of the ponds are tapped by small, man-made, irrigation canals, but, so far as I know, these are not connected to the river. The ponds have permanent water and are often separated by several miles of arid environment. Overland dispersal between waterways is possible in time of flooding. Local residents tell of the infrequent sale of softshells in Cuatro Ciénegas, which hints at their dispersal via the agency of man. The underlying gypsum substrate of the valley has been subjected to considerable erosion; the ponds observed have deep holes, and small caverns and grottos. There are conflicting reports concerning subterranean connections between ponds. Possibly there are underwater connections between some ponds and the headwater streams of the Río Mesquites. Whatever the dispersal route for *emoryi* into the ponds has been, it is strange that the same route has not been traversed by *ater*, permitting its occurrence in the Río Mesquites.

On the basis of morphological criteria, I suspect that *ater* and *emoryi* are genetically compatible. Possibly there is only sporadic entrance of *emoryi* into the ponds inhabited by *ater*, or the accessible dispersal routes for *emoryi* have been relatively recent and there has been insufficient time for genetic adaptation. *T. ater* is maintained as a full species because of the occurrence of two distinct males (KU 46907, *emoryi*, and KU 46911, *ater*) in the same pond (Tío Candido, the type locality). These two specimens are contrasted in a photograph accompanying the type description (Webb and Legler, 1960:Pl. II). The restricted distribution of *ater*, and its characteristics suggest a relict population derived from a *ferox*-like ancestor that may be in the process of becoming extinct.

There are two specimens in the CNHM recorded from Cuatro Ciénegas. One is a female (CNHM 55661) having a plastral length of 19.0 centimeters, and no specific locality other than Cuatro Ciénegas. I examined this specimen before I knew of the existence of *ater*, and noted no unusual features; I have not re-examined the specimen. It is considered representative of *emoryi*. The second is a hatchling (CNHM 47367) having a plastral length of 3.2 centimeters, recorded from Cuatro Ciénegas, Anteojo. The carapace is dark tan having small whitish dots intermixed with a few indistinct, small, blackish specks posteriorly. The specimen is indistinguishable from *emoryi*.

Specimens examined.—Total 12, as follows: COAHUILA: KU 46903-06, 46908-12, 53755-56, 16 km. S Cuatro Ciénegas; UI 73510, 5.7 mi. W Cuatro Ciénegas.

Records in the literature.—Schmidt and Owens (1944:103) record *emoryi* from Cuatro Ciénegas (no museum numbers listed); presumably their reference is to CNHM 55661.

Trionyx muticus Lesueur

Smooth Softshell

Range.—United States from extreme western Pennsylvania, southern Minnesota and South Dakota south to the Gulf of Mexico in Alabama, the western end of the panhandle of Florida, and the eastern half of Texas (see map, Fig. 22.)

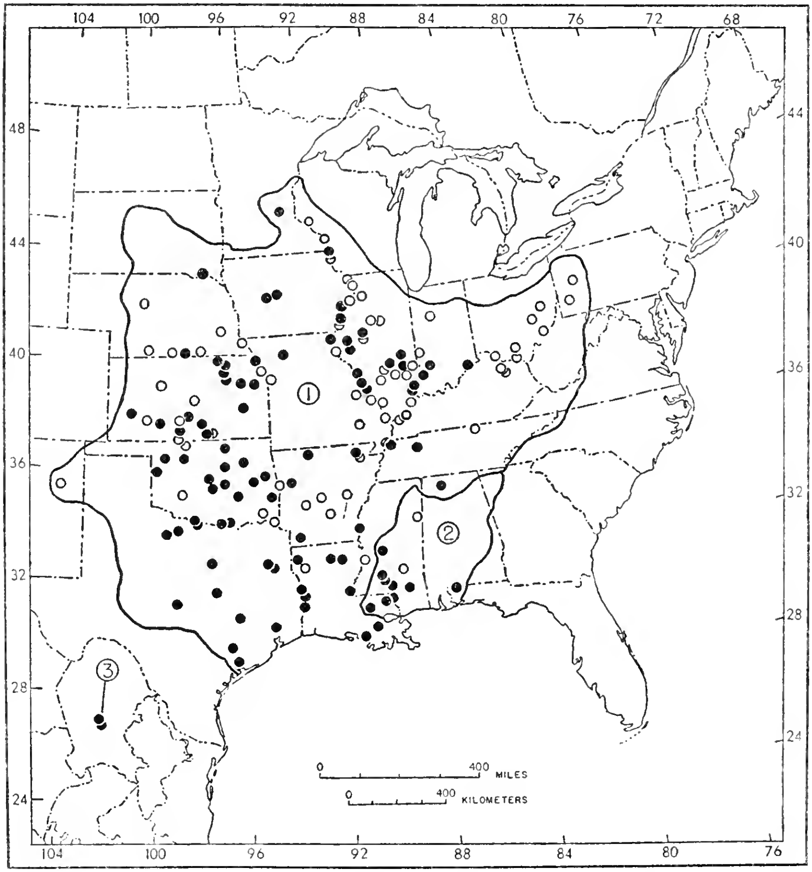


FIG. 22. Geographic distribution of *Trionyx ater* and *Trionyx muticus*. 1. *T. muticus muticus*. 2. *T. muticus calvatus*. 3. *T. ater*.

Diagnosis.—Septal ridges absent; anterior edge of carapace smooth, lacking prominences; juvenal pattern of large dusky spots (sometimes ocellate), or small dusky (not black), dots and short lines; side of head usually devoid of markings except for pale, usually uninterrupted, postocular stripe.

Size small; head narrow; snout long; ventral surface of supraoccipital spine broad proximally, lacking median ridge; foramen magnum evenly rounded, ovoid; opisthotic-exoccipital spur absent; distal part of opisthotic wing truncate; lateral condyle of articular surface of quadrate tapered posteriorly, smaller than medial articular surface; angle of epiplastron obtuse, approximately 100 degrees; callosity on epiplastron sometimes covering entire surface; bony bridge wide in relation to length.

Description.—Septal ridges absent; external characteristics variable (see accounts of subspecies); range in length, in centimeters, of plastron of ten largest specimens of each sex, (mean follows extremes), males, 11.8-14.0, 12.3; females, 17.7-21.5, 18.9; ontogenetic variation in PL/HW, mean PL/HW of specimens having plastral lengths 7.0 centimeters or less, 4.16, ranging from 7.1 to 13.0 centimeters, 5.82, and, exceeding 13.0 centimeters, 7.04; little ontogenetic variation in CL/CW, mean CL/CW of specimens having plastral lengths 8.0 centimeters or less, 1.15, and exceeding 8.0 centimeters, 1.16; mean CL/PCW, 1.97; mean HW/SL, 1.22; mean CL/PL, 1.39.

Greatest width of skull usually at level of squamosal (79%); foramen magnum ovoid; opisthotic-exoccipital spur usually absent (97%); distal part of opisthotic wing truncate, sometimes visible in dorsal view; lateral condyle of articular surface of quadrate tapered posteriorly, smaller than medial articular surface; maxillaries not in contact above premaxillaries; combination of seven neurals, seven pairs of pleurals, and contact of seventh pair of pleurals (38%), or eight neurals, seven pairs of pleurals, and separation of seventh pair of pleurals (41%); angle of epiplastron obtuse, greater than 90 degrees; callosities well-developed, frequently on preplastra and epiplastron of adults.

Comparisons.—The absence of septal ridges distinguishes *muticus* from *ferox*, all subspecies of *spinifer*, and *ater* (ridges are reduced in males of *ater*). The smooth anterior edge of the carapace distinguishes *muticus* from all other American kinds except *ater* and some individuals of *T. s. emoryi*. *T. muticus* resembles only *ater* and *ferox* in usually lacking a well-defined, contrasting pattern of blackish marks on the dorsal surface of the limbs. *T. muticus* resembles *ferox* and differs from *spinifer* and *ater* in lacking a gritty or "sandpapery" carapace on adult males. Adult males of *T. muticus calvatus* and some individuals of *T. m. muticus* from the Colorado River in Texas further resemble *ferox* in having postocular stripes with thick black borders.

T. muticus is the smallest species in North America; the maximum size of the plastron in adult males is approximately 14.0 centimeters (16.0 cm. in *spinifer*) and of adult females 21.5 centimeters (31.0 cm. in *spinifer*). Males and females of *muticus* are sexually mature at approximately the same size as some *T. s. emoryi*; also, the great development of the plastral callosities in *muticus* corresponds to that in some *emoryi*. The head is narrower in *muticus* than in *ferox* or *spinifer*. The carapaces of specimens of *muticus* exceeding plastral lengths of 8.0 centimeters are wider than those of *ferox*, *ater*, *T. s. emoryi* and *T. s. guadalupensis* of corresponding size. *T. muticus* differs from *ater* and three subspecies of *spinifer* (*pallidus*, *guadalupensis*, *emoryi*) in having the carapace widest at a plane approximately one-half the length of the carapace. The snout is longer in *muticus* than in *ferox* and *spinifer*. *T. muticus* differs from *ferox* but resembles *spinifer* in having a relatively short plastron.

The skulls of *muticus* differ from those of *ferox* but resemble those of *spinifer* in usually having the skull widest at the level of the squamosals. Skulls of *muticus* resemble those of *ferox* but differ from those of *spinifer* in usually lacking a well-developed opisthotic-exoccipital spur. Skulls of *muticus* are different from those of *ferox* and *spinifer* in having the 1) ventral surface of the supraoccipital spine widest proximally, lacking a medial ridge, 2) foramen magnum ovoid, 3) distal part of opisthotic wing truncate, 4) lateral condyle of articular surface of quadrate tapered posteriorly, smaller than medial articular surface, and 5) maxillaries not in contact above premaxillaries.

Plastrons of *muticus* differ from those of *spinifer* and *ferox* in having an obtusely-angled epiplastron, relatively large callosities in adults, and a wide hyo-hypoplastral bridge (in relation to length).

Remarks.—Agassiz (1857:399) regarded Lesueur's *Trionyx muticus* as the type species of the genus *Amyda* and the only species known to belong to the genus *Amyda*. Stejneger (1944:7, 9, 12) proposed the generic name *Euamyda* as a new name for the North American *Amyda mutica* as understood by Agassiz. *Euamyda* was proposed for use only if Agassiz's understanding was found to be correct. Actually, Stejneger thought that the Old World and New World kinds concerned were congeneric, and that the type species of the genus *Amyda* was the Old World species *Amyda javanica* Schweigger (= *Testudo cartilaginea* Boddaert).

If *Trionyx muticus* Lesueur is considered to be generically distinct from other soft-shelled turtles, *Euamyda* Stejneger, 1944, is available as a generic name with *Trionyx muticus* Lesueur, 1827, as the type species (by monotypy).

Geographical variation.—*Trionyx muticus* shows no obvious character gradients; the variation is mostly discontinuous and unlike that in *T. spinifer.* On the basis of differences in the juvenal pattern and pattern on head, *T. muticus* can be divided into two subspecies.

Trionyx muticus muticus Lesueur

Midland Smooth Softshell

Plates 45, 46, and 53

Trionyx muticus Lesueur, Mém. Mus. Hist. Nat. Paris, 15:263, pl. 7, December 1827.

Trionyx muticus muticus Webb, Publ. Mus. Nat. Hist. Univ. Kansas, 11:520, August 14, 1959.

Potamochelys? *microcephala* Gray, Proc. Zool. Soc. London, p. 87, 1864.

Type.—Lectotype, Museum d'Histoire Naturelle, Paris, No. 8813; dried carapace and plastron; obtained from the Wabash River, New Harmony, Posey County, Indiana, by C. A. Lesueur in August, 1827 (Pl. 53).

Range.—Central United States; in the Mississippi River drainage from extreme western Pennsylvania, southern Minnesota and South Dakota south to Tennessee, Louisiana and Oklahoma; streams of the Gulf Coast drainage from the Mississippi River in Louisiana westward into Texas including the Colorado River drainage (see map, Fig. 22).

Diagnosis.—Juvenal pattern of dusky dots and usually short lines or bacilliform marks; ill-defined pale stripes on snout usually evident just in front of eyes; pale postocular stripe lacking thick, black borders that are approximately one-half width of pale stripe (except some in the Colorado River drainage of Texas).

Description.—Plastral length of smallest hatchling, 2.1 centimeters (INHS 3458); of largest male, 14.0 centimeters (CNHM 92003); of largest female, 21.5 centimeters (KU 2308).

Juvenal pattern of dusky, grayish marks lacking sharp margins, and usually consisting of both small spots and short streaks or dashes, the former predominating; short streaks or dashes occasionally lacking (TU 14375, Pl. 45, bottom, left; UMMZ 92751); markings variable in number, few and widely spaced, or several and closely approximated (Pl. 45, top, topotypes); pale rim separated from ground color by ill-defined, dusky margin; pattern on adult males well-defined resembling that of hatchlings (TU 16172.1, 16173), scarcely discernable (TU 13294), or absent (TU 1242); mottled and blotched pattern on carapace usually contrasting in large females.

Pale stripes extending forward from eyes usually not more than half distance to tip of snout; inner borders of pale stripes on snout usually absent or dusky and indistinct, occasionally blackish (TU 14606); outer borders of pale stripes darker than inner borders, usually blackish; pale stripes on snout occasionally absent (CNHM 7845, UMMZ 92665, TU 5989, none of these specimens being large females); pale postocular stripe having narrow, dusky or blackish borders (especially UMMZ 92751, TU 14436); pale postocular stripe usually complete, occasionally interrupted having prominent dark-bordered anterior segment just behind eye (TU 14416); lower border of postocular stripe usually in contact with dusky postlabial line; no other markings on side of head; pattern on dorsal surface of soft parts of body not contrasting, composed of closely approximated fine markings that are little darker than background, over-all coloration pale grayish; occasionally, few larger and more constrasting markings on hind limbs (UMMZ 92751, TU 14436).

Underparts white, usually lacking markings; occasional dusky markings on plastral area (UMMZ 110502), dark spots or flecks on undersurface of carapace (BCB 6043, UMMZ 92666), or markings on throat (UMMZ 95032).

Surface of carapace smooth in adult males; large females lacking prominences posteriorly in center of carapace or in nuchal region; anterior edge of carapace smooth in both sexes, but occasionally having regularly spaced furrows or wrinkles (Fig. 8g).

Variation.—Short dusky lines and streaks seem to be lacking from the juvenal pattern on the carapace more often in southern populations (Gulf Coast drainage of Texas) than in northern populations (Mississippi River drainage). I have seen one female, KU 48229 (Pl. 46, bottom, left), plastral length 14.5 centimeters that retained a well-defined juvenal pattern, and lacked a mottled and blotched pattern.

Color notes from life of 11 turtles, KU 55296-306, (eight adult males, three immature females) from the Kansas River at Lawrence, Douglas County, Kansas, are: Buff-yellow rim of carapace, sometimes having pale orange tinge; dusky, dark brown markings on pale brown or tannish carapace of males; dark and pale brown mottled and blotched pattern on carapace of females (smallest specimens having plastral length, 11.0 cm.), many having orangish or buffy hue; soft parts of body brownish to olive-green dorsally, many having small, blackish marks on hind limbs; webbing of limbs yellowish; pale orange, some yellow, laterally at juncture of dark dorsum and pale ventrum (to a lesser extent on hind limbs); pale orange in some suffusing onto dorsal surface of soft parts of body; black-bordered postocular stripes in males having orangish tinge (pattern somewhat obscured in females); whitish ventral surface in some having pale orangish tinge here and there; many having dusky, grayish flecking on plastral area and anterior ventral surface (most intense on 55306 giving appearance of grayish suffusion).

I have seen only three specimens from the Colorado River drainage in Texas. Two of these (UMMZ 92751, TU 14436) are characterized by much black pigmentation. A contrasting pattern of relatively large black marks occurs on the dorsal surface of the soft parts of the body, especially on the hind limbs, and the pale postocular stripes have thick black borders. UMMZ 92751, having a plastral length of 5.5 centimeters, has a juvenal pattern of widely-spaced dark dots that lacks short lines. The other *muticus* from the Colorado River (CM 3055), a large female 19.0 centimeters in plastral length, has ill-defined postocular stripes lacking dark borders, although a small dusky blotch occurs on the right side of the head.

Comparisons.—*T. m. muticus* differs from *T. m. calvatus* in having pale stripes on the snout, a juvenal pattern of small dusky spots (usually lacking ocellate spots) and short lines, and a pale postocular stripe lacking thick, blackish borders (except in some turtles from the Colorado River system of Texas). One unique characteristic of *muticus* is the short, dusky lines in the juvenal pattern; these marks, however, are occasionally absent.

Remarks.—*Trionyx muticus* generally has been considered a distinct species since its description by Lesueur (1827:263-66, Pl. 7); Wied-Neuwied (1865: 53), at least, questioned the identity of *muticus*, believing it to be based on a secondary sexual difference of *T. spiniferus*. Lesueur did not designate a type in the description, and mentioned that he had seen only three specimens (*op. cit.*:264). Stejneger (1944:17-18) discussed two mounted specimens (Nos. 787 and 788) in the Natural History Museum at Paris, and mentioned that No. 787 was designated ". . . as the type on the printed label (although presumably not done by Lesueur)." Dr. Jean Guibé (*in litt.* September 24, 1959) informed me that Nos. 787 and 788 are numbers without value and correspond, respectively, to catalog numbers 8813 and 8814. In addition, the Museum possesses an alcoholic specimen, No. 564, obtained by Lesueur from the Wabash River, that seems to have been acquired by the museum after the publication of the original description. No. 8813 is regarded as a lectotype.

Gray (1864:87) described the species *microcephalus* and questionably included it in the genus *Potamochelys* Fitzinger, 1843; the locality was stated as "Sarawak (Wallace)." Gray especially noted the small elongate head and believed that the acquisition of adult specimens would prove that it belonged to a new genus. Later, Gray (1869:221) proposed the generic name *Callinia* as a new name for *Aspidonectes* as understood by Agassiz (1857:403). Gray referred *microcephala* to *Callinia* (*op. cit.*:214, 222) and recognized also *Amyda mutica* (*op. cit.*:212). Baur (1888:1121) remarked that "*Callinia microcephala* Gray, of the British Museum, with the locality Sarawak, is *Amyda mutica* Les." The species *microcephalus* has since been considered a synonym of *Trionyx muticus*. Schmidt (1953:110) designated the type locality as New Harmony, Indiana.

Müller (1878:641) listed the species *Trionyx muticus* from México as follows: "*b. in Alcohol. Mexico. 1872. [2]." Smith and Taylor (1950:18, footnote) wrote that the record required confirmation. Webb and Legler (1960:24) questionably referred this record to the synonomy of *T. ater*, which resembles *muticus*. *T. muticus* is not known to occur in México. According to Dr. Lothar Forcart (*in litt.*) of the Naturhistorische Museum in Basel, Switzerland, only one specimen on which Müller based his record is extant. My examination of this specimen reveals that it is a hatchling *T. s. emoryi*, plastral length 3.5 centimeters, bearing catalog number 1032; there are no additional data of collection.

Strecker and Williams (1927:16) mentioned one specimen of *muticus* that was obtained at Christoval, Tom Green County, Texas, and I presume this is the basis for Pope's mention of this species from Tom Green County, Texas (1949:319). Although I do not doubt that *T. muticus* occurs in Tom Green County, this record possibly is based on *T. spinifer* because, 1) there are no specimens of *muticus* in the Strecker Museum from Tom Green County, but there is one specimen of *spinifer* (SM 3282), and in none of Strecker's publications is there any mention of *spinifer* from Tom Green County, and 2) Strecker had, at least once, misidentified the two species; his record of *muticus* from Wallace Bayou, Louisiana (Strecker and Frierson, 1926:last page, no numbers), represents *T. spinifer pallidus* (SM 2374-75).

Specimens examined.—Total 261, as follows: Alabama: *County unknown:* USNM 118167, Wheeler Reservoir, Tennessee River.

Arkansas: *Franklin:* KU 19459-60, Ozark. *Lafayette:* KU 2938, 3057, Lewisville. *Lawrence:* CNHM 92003, Imboden; CNHM 92005, Powhatan; USNM 59214, Black River, Black Rock. *Marion:* TU 14606 (2), White River at Cotter. *Prairie:* KU 1831, 1868, 1870, 1874-76, 1930-31, 1957-63, 2294-302, 2305-06, 2308-09, 2838-41, 3002, White River, DeVall's Bluff.

Kansas: *Barber:* USNM 95185-86, 1 mi. S Lake City. *Doniphan:* KU 1872, 1878, 1964, Doniphan Lake. *Douglas:* KU 2220, 16148, 23230, 40179, 50825-26, 55296-306, Kansas River, Lawrence; KU 45065-66, 1 mi. N, 1.5 mi. W Lakeview. *Ford:* KU 51516, Ford. *Kearny:* KU 48216, 4 mi. S, 1.5 mi. W Deerfield. *Marshall:* KU 48228, Blue Rapids. *Pottawatomie:* KU 48229-33, 48238, 2 mi. E Manhattan, Riley County. *Reno:* USNM 95260, 6 mi. E Turon. *Riley:* KU 46861, 48234-35, 4 mi. N Manhattan; KU 48236, 2 mi. NE Randolph. *Sedgwick:* UMMZ 95362, Wichita. *Shawnee:* UMMZ 95366-67, Topeka. *Sumner:* USNM 95415, 3 mi. SE Oxford. *Washington:* KU 48237, 8 mi. S Hanover. *Woodson:* KU 45064, 1 mi. E, 2 mi. S Neosho Falls. *County unknown:* USNM 51528.

Illinois: *Cass:* INHS 2146, Beardstown. *Coles:* INHS 1965-67, 3 mi. S Charleston. *Jackson:* INHS 5894, 6.5 mi. N Aldridge, Union County; UMMZ 81570, Mississippi River. *Jasper:* INHS 2412, Rose Hill. *Jersey:* INHS 2156-58, Grafton. *Mason:* INHS 2147, Cedar Creek. *Mercer:* INHS 3458, Keithsburg. *Monroe:* INHS 4088, 3 mi. NE Columbia. *Morgan:* CNHM 6028, INHS 2148, Meredosia. *Pope:* CNHM 2463 (30), Golconda. *Schuyler:* UI 40-41, Crooked Creek. *Shelby:* INHS 2283, Holliday. *Wabash:* INHS 5228, Mt. Carmel.

Indiana: *Daviess:* UMMZ 110234, White River, 1.5 mi. W Elnora. *Jefferson:* USNM 8337, Madison. *Knox:* UMMZ 111880-81, "near" Decker Chapel. *Posey:* INHS 7278-80, 7447, TTC 798, Wabash River, 2-2.5 mi. S New Harmony; UMMZ 110598, 8 mi. NW Mt. Vernon.

Iowa: *Allamakee:* UMMZ 92657, ¼ mi. W Victory, Vernon County, Wisconsin; UMMZ 92658-64, Mississippi River, "near" Lansing. *Boone:* UMMZ 92665, Des Moines River at Ledge State Park. *Greene:* UMMZ 92666, 3.5 mi. N Scranton. *Muscatine:* USNM 53521, 54733-34, 54742, 60054-56, Fairport.

Louisiana: *Beauregard:* TU 1242, Sabine River, Merryville. *Caddo:* CNHM 7845, Gayles. *Catahoula:* USNM 113228, Jonesville. *Concordia:* USNM 99870, Red River, "near" Shaw. *Ouachita:* TU 5989, Monroe. *Richland:* USNM 100422, Rayville. *Sabine:* TU 13163, 13294, Sabine River, 8 miles SW Negreet. *St. James:* TU 7543, Vacherie. *St. Mary:* USNM 100406, Berwick Bay, "near" Morgan City. *Vernon:* KU 41380, 46777, Sabine River NW Burr Ferry.

Minnesota: *Hennepin:* AMNH 4761-62, Fort Snelling.

Mississippi: *Washington:* USNM 92605, Greenville. *County unknown:* USNM 115939.

MISSOURI: *Clark:* USNM 59267, 59278, Alexandria. *Daviess:* UMMZ 95505, Grand River, 1 mi. S Jameson. *St. Louis:* SM 2052, St. Louis. *Wayne:* UMMZ 82823, St. Francis River.

NEBRASKA: *Webster:* UMMZ 89526, Republican River, 2 mi. E Inavale.

OKLAHOMA: *Cleveland:* OU 5480-81, 6473, South Canadian River, 4 mi. SE Norman. *Hughes:* KU 50845, 4 mi. N Atwood. *Kay:* OU 9741, 8 mi. E Ponca City. *Le Flore:* OU 2148; OU 27390, Poteau River below Wister Dam. *Love:* OU 27472, Hickory Creek, 9 mi. E Marietta. *Major:* OU 8597, 7 mi. E Orienta. *Marshall:* KU 50827-29, 50848, 50853, OU 27593-94, TU 16077 (4), Lake Texoma, 2 mi. E Willis. *McIntosh:* OU 8993, 4 mi. W Onapa. *Oklahoma:* OU 10137, Lake Oberholser. *Payne:* UMMZ 89629, Cimarron River, 3 mi. E Ripley; UMMZ 90002, 19 mi. SE Stillwater. *Pottawatomie:* OU 25176-83, South Canadian River, 5 mi. SW Shawnee. *Roger Mills:* OU 12472. *Sequoyah:* OU 9006, Illinois River, 2 mi. NE Gore. *Tulsa:* UMMZ 95032 (4), Arkansas River at Tulsa. *Woodward:* CNHM 15472-73; OU 8599-600, 5 mi. E, 1 mi. N Woodward.

SOUTH DAKOTA: *Yankton:* UMMZ 110499-500, Missouri River at Fort Randall; UMMZ 110501-02, Missouri River at Yankton.

TENNESSEE: *Benton:* UMMZ 53198, Trotter's Landing. *Lake:* USNM 102677, Reelfoot Lake. *Obion:* USNM 102910, Reelfoot Lake.

TEXAS: *Archer:* TU 16173, Lake Diversion. *Baylor:* TU 16172 (2), Lake Kemp. *Brazos:* TCWC 7250, Bryan. *Clay:* TCWC 7248-49, 7259-61, 8 mi. NW Ringgold, Montague County; TU 16667, 3 mi. W Byers. *Grayson:* UI 2419, Lake Texoma. *Gregg:* SM 6685, near Gladewater; USNM 22629, Sabine River, 5 mi. S Longview. *Liberty:* TU 14416, 14375, Trinity River, "near" jct. with Big Creek. *McLennan:* BCB 6030, 6043, SM 2557, 2561, Lake Waco. *Matagorda:* CM 3055, Colorado River, Bay City. *San Saba:* TU 14436, San Saba River, 11 mi. NNW San Saba. *Tarrant:* UMMZ 92750, Worth Lake, Fort Worth. *Wharton:* UMMZ 92751, Colorado River, Wharton.

NO DATA: MCZ 1594 (erroneously recorded from Mobile, Alabama); USNM 029261, 59982.

Records in the literature.—ARKANSAS: *Garland:* Hot Springs (Combs and Hurter *in* Strecker, 1924:47). *Jefferson:* Pine Bluff. *Pulaski:* Little Rock. *Sebastian:* Fort Smith (Hurter and Strecker, 1909:21).

ILLINOIS: *Adams:* Quincy (Garman *in* Cahn, 1937:179). *Alexander:* Horseshoe Lake (Cahn, *loc. cit.*); Cairo (Garman *in* Cahn, *loc. cit.*). *Carroll:* 5 mi. S Savanna (Stejneger, 1944:24). *Clay:* Louisville. *Clinton:* Carlyle. *Crawford:* Robinson (Cahn, *loc. cit.*). *Cumberland:* Embarrass River (Peters, 1942:183). *Fayette:* Vandalia. *Gallatin:* Shawneetown (Cahn, *loc. cit.*). *Hancock:* between Warsaw and Hamilton (Stejneger, *op. cit.*:23). *Jackson:* Murphysboro. *Jasper:* Newton. *Marion:* Centralia. *Mason:* Havana. *Massac:* symbol on map. *Menard:* Petersburg. *Peoria:* Peoria. *Randolph:* Chester (Cahn, *loc. cit.*). *Richland:* Olney (Stejneger, *loc. cit.*). *Rock Island:* Rock Island. *St. Clair:* East St. Louis (Cahn, *loc. cit.*). *Union:* (Cagle, 1942a:199). *White:* Carmi. *Whiteside:* Sterling (Cahn, *loc. cit.*). *Woodford:* Mackinaw Creek (Garman *in* Cahn, *loc. cit.*).

INDIANA: *Carroll:* "near" Delphi (Agassiz, 1857:400). *Vigo:* Terre Haute (Blatchley, 1891:22).

IOWA: *Des Moines:* "near" Burlington (Agassiz, 1857:400). *Dubuque:* Mississippi River, 8 mi. S Dubuque (Goldsmith, 1945:447). *Lee:* Keokuk (Stejneger, 1944:23).

KANSAS: *Barber:* 5 mi. SE Lake City; Salt River, S of Aetna (Burt, 1935:321). *Cowley:* symbols on map (Smith, 1956:157). *Gray:* Arkansas River, 1 mi. W Cimarron (Clarke, 1956:215). *Leavenworth:* Missouri River, Fort Leavenworth (Brumwell, 1951:207-08). *McPherson:* Lindsborg (Breukelman and Smith, 1946:112). *Pratt:* State Fish Hatchery, "near" Pratt (Taylor, 1933:269). *Trego:* Wakeeney (Stejneger, 1944:24).

KENTUCKY: *Fleming:* Fox. *Rowan:* Triplett (Welter and Carr, 1939:130). *County unknown:* Ohio River (Funkhouser, 1925:71).

LOUISIANA: *De Soto:* Bayou Pierre (Strecker and Frierson, 1926:last page, no numbers).

MINNESOTA: *Houston:* Brownsville (Breckenridge, 1944:183). *Winona:* Homer (Stejneger, 1944:23).

MISSISSIPPI: *Warren:* Vicksburg (Cook, 1946:185).

MISSOURI: *Jackson:* Fry's Lake (Anderson, 1942:219). *Jefferson:* Meramec River (Boyer and Heinze, 1934:199). *County unknown:* Osage River (Agassiz, 1857:400).

NEBRASKA: *Franklin:* ½ mi. S Franklin; 1 mi. SE Naponee. *Furnas:* 4 mi. E Cambridge. *Lancaster:* Lincoln. *Nemaha:* Peru. *Thayer:* (Hudson, 1942: 102). *Thomas:* (Smith, 1958:36).

NEW MEXICO: *San Miguel:* Conchos River above Conchos Dam (Shields and Lindeborg, 1956:120).

OHIO: *Brown:* mouth White Oak Creek, Higginsport. *Muskingum:* "near" Gaysport. *Pike:* Scioto River in Camp Creek, Newton and Scioto Twps.; Pike Lake. *Scioto:* Scioto River in Clay and Rush Twps.; Scioto River, Portsmouth; Scioto River, 3 mi. N Rushtown. *Tuscarawas:* Tuscarawas River, 2 mi. below Gnadenhutten; "near" Winfield. *Washington:* Dam No. 2, Muskingum River, northern edge of Marietta; Ohio River, 4 mi. SE Marietta (Conant, 1951:156, 264).

OKLAHOMA: *Alfalfa:* 6.5 mi. NE Ingersoll. *Comanche:* Camp Boulder, Wichita National Forest (Ortenburger and Freeman, 1930:188). *McCurtain: Pushmataha:* (Ortenburger, 1927:100).

PENNSYLVANIA: *Allegheny:* Neville Island, Ohio River below Pittsburgh (Atkinson, 1901:154). *Clarion:* Allegheny River at Foxburg (Netting, 1944:85).

?SOUTH DAKOTA: *County unknown:* Fort Mackenzie, Missouri River, 6-8 mi. below Cedar Island (Stejneger, 1944:15).

TENNESSEE: *Lake:* Mississippi River (Parker, 1948:29). *Pickett:* Obey River at Eagle Creek Ford (Shoup, Peyton and Gentry, 1941:75).

WISCONSIN: *Crawford: Pepin:* Mississippi River (Breckenridge, 1944:183; Pope and Dickinson, 1928:82).

Trionyx muticus calvatus Webb

Gulf Coast Smooth Softshell

Plate 47

Trionyx muticus calvatus Webb, Univ. Kansas Publ. Mus. Nat. Hist., 11:519, 1 fig., 2 pls., August 14, 1959.

Type.—Holotype, UI 31071, hatchling, sex undetermined, alcoholic; obtained from Pearl River, Roses Bluff, 14 miles northeast Jackson, Rankin County, Mississippi, by William F. Childers on August 25, 1952.

Range.—Southeastern United States from the Florida Parishes of Louisiana eastward to the western end of the panhandle of Florida; rivers of the Gulf Coast drainage from the Escambia River drainage, Florida, westward to Louisiana and Mississippi including the Pearl River drainage. The eastern extent of geographic range is not known (see map, Fig. 22).

Diagnosis.—Juvenal pattern of large circular spots, often ocellate; no stripes on dorsal surface of snout; pattern on dorsal surface of limbs of fine markings, not in contrast with ground color; pale postocular stripes having thick black borders approximately one half width of pale stripe on adult males.

Description.—Plastral length of smallest hatchling, 3.0 centimeters (TU 17301); of largest male, 11.8 centimeters (KU 47118); of largest female, 18.0 centimeters (TU 13473).

Juvenal pattern of dusky, circular spots, some ocellate, lacking short lines and streaks; number of spots variable; some spots on carapace of hatchlings may have maximum diameter of three millimeters (TU 17301); pale rim of carapace having dusky, ragged, inner border; juvenal pattern on adult males absent or usually evident, at least posteriorly (TU 17306.1).

Dorsal surface of snout lacking pale stripes just in front of eyes; pale postocular stripe having thick, black borders on adult males, but narrower, dusky or blackish borders on juveniles and large females; lower border of postocular stripe usually in contact with dusky postlabial line; no other markings on side of head; pattern on dorsal surface of soft parts of body of closely approximated, fine markings that are not in contrast with ground color, over-all coloration grayish; occasionally few larger and more contrasting markings, especially on hind limbs and anteriolateral surface of forelimbs.

Underparts whitish, lacking markings, occasional black flecks or dusky marks posteriorly along ventral edge of carapace (TU 17306.3).

Surface of carapace smooth in adult males; large females lacking prominences posteriorly in center of carapace or in nuchal region; anterior edge of carapace smooth in both sexes, but occasionally having regularly spaced furrows or wrinkles on hatchlings.

Comparisons.—*T. m. calvatus* can be distinguished from *T. m. muticus* by the absence of pale stripes on the snout just in front of the eyes, in having pale postocular stripes that have thick, black borders on adult males, and in having a juvenal pattern of large, circular spots that are often ocellate and three millimeters in diameter (no short lines).

Remarks.—I have not seen specimens of *calvatus* from the Tombigbee-Alabama river drainage; presumably Cook's record (1946:185) from Lowndes County, Mississippi, represents this subspecies.

It is still not certain that *calvatus* occurs in streams that drain into Lake Pontchartrain, Louisiana; TU 17236 from the Amite River that lacks a diagnostic character is questionably referred to *calvatus* (Webb, 1959:524). As mentioned previously *T. s. asper* shows little evidence of intergradation with *T. spinifer* in the Mississippi River drainage; *asper* is present in streams of the Lake Pontchartrain drainage. *T. m. calvatus* presumably shows a corresponding relationship with *T. m. muticus* in the Mississippi River drainage. There are no specimens that indicate intergradation between *calvatus* and *muticus; calvatus* is expected in streams that drain into Lake Pontchartrain, Louisiana. Probably *calvatus* occurs eastward in the Apalachicola drainage system.

Specimens examined.—Total, 38 as follows: FLORIDA: *Escambia:* KU 47116, 50852, 50854-55, 50835-36, TU 13473, 16682, 17301, 17302 (2), Escambia River, 2 mi. E, 1 mi. N Century.

LOUISIANA: *East Baton Rouge:* TU 17236, Amite River, "near" Baton Rouge. *Washington:* TU 13795, Bogue Chitto River, Enon; TU 17303 (5), TU 17304 (4), Pearl River, "near" Varnado. *No data:* TU 17305.

MISSISSIPPI: *Lawrence:* KU 47117-19, TU 16956, USNM 7655, Pearl River within 4 mi. of Monticello; TU 17306 (4), Pearl River, 9 mi. S Monticello. *Marion:* USNM 95133-34, Pearl River, Columbia. *Perry:* MSC uncatalogued (3), 3 mi. SE New Augusta. *Rankin:* UI 31071, Pearl River, Roses Bluff, 14 mi. NE Jackson.

Records in the literature.—MISSISSIPPI: *Forrest:* no data. *Jones:* Crawford Bridge. *Lowndes:* Columbus, Lake Park (Cook, 1946:185).

NATURAL HISTORY

Habitat

Most writers who describe the general habitat of soft-shelled turtles mention large rivers and streams having some current, and large permanent, quiet bodies of water having soft mud or sand bottoms, but note the general avoidance of temporary water. The impermanence of water in the ponds and "charcos" of headwaters of streams may preclude the presence of softshells from these otherwise suitable habitats. Seemingly, soft-shelled turtles are not restricted to particular local situations or microhabitats in a continuous aquatic environment as are some kinds of fish, which seem to be more or less confined to riffle areas or deep holes. Certain activities of softshells such as burying themselves in soft sand in shallow water or seeking crawfish and other food over a gravel-rock substrate or one that is débris-laden, are best carried on in different habitats. Repeated observations of turtles that are probably engaged in a specific activity in a restricted area may lead to erroneous general conclusions regarding the over-all preference for a specific habitat. Perhaps this accounts for Conant's statement (1951:156) that "In the lower portion of the Scioto River [Ohio] it appears that the present species [*muticus*] is abundant while *spinifer* is almost entirely absent."

Cagle (1954:181) wrote that softshells "inhabit the extreme headwaters and smaller tributaries." Other statements in the literature indicate the variety in kinds of habitat. In Louisiana, Beyer (1900:44) mentioned *spinifer* as abundant "in all inland waters, preferring, however, such bayous which have sloping and sandy banks upon which they are fond of sunning themselves." Viosca (1923:41) reported soft-shelled turtles as characteristic "of the large silt-bearing rivers . . . such as the Pearl, Amite, Mississippi and Atchafalaya." Cagle and Chaney (1950:386) wrote that *spinifer* in Louisiana was found in greatest abundance in streams having some current, but that individuals were also common in quiet areas; the habitats recorded were: False River—a lake of clear water supporting an abundance of submerged vegetation, the shallow ends having mats of water hyacinth; Lakes Iatt and Bistineau—cypress swamps having clear or muddy water; Caddo Lake—a large lake having a light oil film on the surface of the water, and vegetation toward the shore consisting of cattails, water lilies and water hyacinths, and along the bank of cypress and willow trees; Caddo Lake Spillway—muddy with swift current; Sabine River—swift current, traps set in quieter backwater areas or near cypress logs in river; Lacassine Refuge—traps set in inlets and coves of ship channel having vegetation of water hyacinth, alligator grass, and along bank, saw grass, cypress knees and snags. Stejneger (1944:59) reported *spinifer* taken in barrow pits in Mississippi.

In Southern Illinois, Cagle (1942:160) recorded *spinifer* in drainage ditches (normally having several feet of water and a lush growth of aquatic vegetation) that connect inland swamps to the Mississippi floodplain but dry up periodically, and in Elkville Lake, an artificial lake having much aquatic vegetation in shallow areas (*op. cit.*:157). Myers (1927:339) recorded a *spinifer* from Indiana from a "tiny brook." In east-central Illinois P. W. Smith (1947:39) recorded *spinifer* in mud-bottomed dredge ditches, lakes, ponds, small streams and rivers, whereas *muticus* was found to prefer rivers having clean, sandy bottoms and was not taken from lakes or small streams. This restriction in habitat preference of *muticus* is again emphasized by Smith and Minton (1957: 346) who wrote that in Illinois and Indiana, *muticus* "generally avoids lakes and minor streams." Weed (1923:48), however, recorded *muticus* (and *spinifer*) from Meredosia Bay, Illinois, presumably a broad, shallow, muddy ox-bow lake of the Illinois River.

In Minnesota, *spinifer* has been taken from the Mississippi River, which is described as fairly swift having a fluctuating water level, sandy islands, mud banks, a bed of pebbles and large boulders, and abundant crawfish (Breckenridge, 1955:5). In Michigan, Edgren (1942:180) recorded *spinifer* from a "very small muck-bottomed lake." Evans and Roecker (1951:69) recorded *spinifer* from Long Point, Lake Ontario, which is a "broad sand spit, straight on the lakeward side but irregular with wet flats and lagoons on the bayside."

In Kansas, Brumwell (1951:207-08) found "mostly young [*muticus*] . . . in the old ponds left during flood stages of the Missouri River" . . . and *spinifer* occasionally . . . "in the backwaters where stagnant ponds had been formed." In south-central Kansas, Burt (1935:321) reported *muticus* from "a sandbar at junction of a small creek and Medicine River" . . . and . . . a "shallow sand-bottomed, algae-filled pasture streamlet." The same author reported *spinifer* from a "sand-bottomed prairie streamlet" . . . and . . . "an alga-filled pool near a stream." Burt (*loc. cit.*) remarked that "No ecological differences in general habitat and field behavior of *mutica* and *spinifer* are evident in Kansas." Clarke (1958:21) observed *spinifer* in Long Creek (Osage County, Kansas), which is a winding stream, characterized by numerous deep holes alternating with rocky riffles, and having high and wooded banks, and mostly mud bottom but occasional rock bottom.

Marr (1944:490) mentioned a *spinifer* that was obtained on the bank of a small, mud-bottomed stream in the Texas panhandle, and Linsdale and Gressitt (1937:222) recorded *spinifer* from irrigation canals in Baja California.

In southern Florida, *ferox* occurs in all fresh water habitats (Duellman and Schwartz, 1958:272). Carr (1940:107) reported *ferox* as widely distributed in streams, lakes, big springs and canals. Judging from the numbers of turtles, "the larger canals in the Everglades must represent something like an optimum habitat" (Carr, 1952:417). Wright and Funkhouser (1915: 119) wrote that in the Okefinokee Swamp, *ferox* was especially abundant where the water is deep and the bottom soft, and the species was found wherever there were alligators. Deckert (1918:31) wrote that young *ferox* were taken in springs and brooks near Jacksonville, Florida. Marchand (*in* Carr, 1952:417-19) observed *ferox* while water-goggling in Florida and noted that individuals buried themselves in deep water in white sand, mud or bubbling mud-sand springs, sometimes where there was vegetation overhead.

Neill (1951:16) collected *ferox* in marshes, "prairies," flood-plain lakes, lagoons, ox-bow lakes, mangrove swamps, rivers, creeks, calcareous spring runs, man-made lakes and lime sinks. The same author (*loc. cit.*) reported taking *agassizi* (= *asper*) in large muddy rivers, clear "black-water" streams, calcareous spring runs, creeks, marshes, lagoons, ox-bow lakes, flood-plain lakes, lime sinks, man-made lakes, and smaller ponds. Crenshaw and Hopkins (1955:16), however, stated that in the area where *T. ferox* and *T. spinifer asper* overlap, "*asper* is nearly always an inhabitant of fluviatile situations whereas *ferox* is equally closely confined to non-fluviatile lakes and ponds"; in the region of sympatry, Schwartz (1956:8) reported *ferox* from "a moderately fast, blackwater stream [Combahee River, South Carolina]."

Carr (1952:417) wrote that *ferox* is not uncommon near the mouths of streams in brackish waters, where the tide must occasionally take it to sea, and cited Conant, who told of an individual found at sea in Bahaman waters; Carr (1940:25) listed *ferox* as occasional in the marine-littoral, mangrove swamps, as did Neill (1951:16). Neill (1958:26-27) mentioned his observance of *ferox* at the mouth of the Pithlachascotee River, Pasco County, Florida, where the water is sufficiently saline to favor the growth of oysters, and added that commercial fishermen had told him that these turtles are sometimes netted with loggerhead sea turtles (*Caretta*) in the Indian River. Neill (*op. cit.*:5-6) also noted the presence of *ferox* on Meritt Island, which supports an extensive saltwater herpetofauna, off the coast of Brevard County, Florida. Löding (1922:47) recorded *spinifer* from Fig Island, Mobile County, Alabama, which is probably a marine or brackish water habitat. Cagle and Chaney (1950:386) obtained one *spinifer* in a brackish marsh of the Sabine Wildlife Refuge, Louisiana; the poor trapping returns here (one *Trionyx* and one *Pseudemys* in 408 trap-hours) suggest that fresh-water species are not abundant in brackish habitats. Neill (1958:26-27) has summarized the occurrence of soft-shelled turtles in marine and brackish habitats.

My own observations indicate a variety of habitat preferences; the term "relatively clear" refers to waters in which visibility extends four to six inches below the surface at night using a head-light.

Individuals of *spinifer* have been taken in large, deep rivers having a moderate to swift current, relatively clear water, mostly sand and clay bottoms, and emergent débris intermittent along the shoreline; the banks may be steep and of mud having a sparse growth of herbs (Black Warrior River, south of Tuscaloosa, Alabama), or of low extensive, sandy bars and beaches (Escambia River, near Century, Florida, Pl. 50, Fig. 1). A juvenile *spinifer* was taken by hand among rocks in quiet water behind a rocky shoal in the large, deep-channeled Ocmulgee River (near Hawkinsville, Georgia). Several individuals of *spinifer* were seen in the Flint River (near Bainbridge, Georgia), which had a swift current in a wide, deep channel, sandy or sand-silt banks, few brush piles along shore and many oölitic, submergent snags on an otherwise sandy bottom; the water was exceedingly clear and permitted watergoggling (this habitat has been obliterated by a dam on the Apalachicola River). A large female *spinifer* was taken on a set line from the bottom of one of several deep holes (approximately seven feet) that were connected by shallow areas or riffles (near headwaters of Escambia River—Escambia Creek, Escambia County, Alabama). Two large females of *spinifer* (one escaped) were taken on a trotline set in a large, deep, isolated barrow pit near the Escambia River (near Century, Florida); there was no aquatic vegetation, the water was slightly turbid, and the substrate was of a sand-silt or mud.

In Arkansas, *spinifer* has been taken in large deep rivers having relatively clear water, a moderate current, steep banks four to 15 feet high, and a substrate of mud with few rocks (one taken on trotline, escaped; Black River, near Black Rock, Lawrence County). Two *spinifer* were taken (trotline and hoopnet) from a smaller (approximately 50 feet wide) turbid river having a swift current, débris along the shoreline, and mud-gravel banks (Petit Jean Creek, Yell County). Several *spinifer* and *muticus* were taken from the White River (Marion County) having a sand-gravel or bed rock bottom and clear water; individuals were collected by hand in shallow water (approximately 3½ feet deep) as they lay on the bottom in the main channel where the current was moderate to swift or in a quiet-water side channel having submergent vegetation.

Lake Texoma, an impoundment on the Red River, having a fluctuating water level with no permanent stand of aquatic vegetation, a mud-rock or sand-silt bottom, and turbid water (Pl. 49, Fig. 1) is a suitable habitat for *spinifer* and *muticus*. *T. spinifer* is found in large rivers having relatively clear water, moderate currents, emergent logs and débris, and mud or sand banks (Little River, McCurtain County, Oklahoma, Pl. 48, Fig. 1), or small, shallow, turbid creeks having sand-gravel channels of pools connected by riffle areas (Mayhew Creek, Choctaw County, Oklahoma).

Three *spinifer* were taken from the Llano River (near Llano, Texas) in a period of low water level in hoop-nets set in a large quiet-water pond about four feet deep and having patches of rushes encroaching into the water from the shore. The river bed of sand, gravel and large boulders consisted of narrower, swift-water channels, small pools and riffles, and large ponds.

Individuals of *T. s. emoryi* have been taken in large ponds having little or no current, turbid, deep water, and clay or sand-gravel banks (Río Purificación, Padilla, Tamaulipas). Two *emoryi* were collected from a large pond (Río Sabinas, near Sabinas, Coahuila), which was connected to an adjoining one by riffle areas and had little or no current, relatively clear, greenish water, clay or mud banks, a sand-gravel bottom, and was flanked by brush and large cypress trees. A few *emoryi* were trapped in hoop-nets that were set in the Río Mesquites, a stream in central Coahuila approximately 20 feet wide and six feet deep, flanked by dense stands of *Phragmites*, and having a moderate current, relatively clear, pea-green water and a mud-sand substrate with some gravel; the stream enlarged in some places to form quiet-water coves (Pl. 48, Fig. 2). One adult male *emoryi* was taken from a crystal clear, dendritic, pond (El Mojarral, near Cuatro Ciénegas, Coahuila), having shallow areas averaging about two feet but several deep holes—in one of these at the west end of the pond the water was being emitted under pressure from an underwater cavern and "bubbling" at the surface; the vegetation consisted of scattered patches of water-lilies and stonewort; the bottom was a soft mud-marl, and in some places was carpeted with shells of small gastropods. This habitat corresponds to that of the type locality of *T. ater* (Pl. 49, Fig. 2); see description in Webb and Legler (1960:26). The water of the ponds is warm; at 8 p. m. on July 31, 1959, the temperature of the water at the type locality of *ater* was 29° C., and the air was 27° C.

An immature female *spinifer* was taken on a trotline in a swift, clear, cold-water habitat having mud banks and an abundance of brush piles (Little Tennessee River, Monroe County, Tennessee). *T. spinifer* occurs also in large ox-bow lakes having relatively clear water, extensive mats of submerged vegetation, a soft mud bottom, and several emergent stumps and fallen logs (Lake Concordia, Concordia Parish, Louisiana); alligator grass and cypress trees encroached to the shoreline.

Locality data of some individuals of *spinifer, hartwegi, asper, pallidus* and *emoryi* that were examined indicated that turtles were captured in ponds, bayous, sloughs, lakes, impoundments, rivers and creeks, indicating habitation of essentially all permanent waters.

A juvenile of *hartwegi* was seen by Mr. Wendell L. Minckley on a gravel bar jutting into a small, shallow creek having a mud-gravel bottom (Carnahan Creek, Pottawatomie County, Kansas); the impounding of the Big Blue River by the Tuttle Creek Dam will obliterate this habitat. Mr. J. Knox Jones, Jr. reported seeing a large softshell in a narrow, shallow, clear sandy creek in Holt County, Nebraska.

T. s. emoryi occurs in large rivers having generally turbid waters, a moderate to swift current and mud or sand bottoms such as the Río Grande; this habitat corresponds to that of large rivers in the western parts of the range of *T. s. pallidus* (Red and Washita) and *T. s. hartwegi* (Canadian and Cimarron). These last-named rivers, in periods of low water level, often have shallow, clear, flowing water in parts of the river bed. *T. s. emoryi* has also been taken from small creeks having bottoms of rocks and large boulders (Black River Village, Eddy County, New Mexico; field notes of Sydney Anderson and Kenneth Shain, June 12-14, 1958).

I received a hatchling *T. s. guadalupensis* that was obtained in a clear, shallow-water stream (Hondo Creek, Bandera County, Texas, on April 12, 1958). The larger streams and rivers known to be inhabited by *guadalupensis* are generally clear having greenish-tinted waters. The geographic distribution of *guadalupensis* indicates that that subspecies occurs principally in those waters that drain the limestone-mantled, Edward's Plateau off the Balcones Escarpment; the headwaters are characterized by clear, calcareous streams having occasional travertine deposits. It is probably this type of habitat to which Agassiz's statement (1857:408) of "clear, bold and rocky streams" refers.

There are a few specimens whose locality data indicate a tolerance of brackish-water habitats. An adult male *spinifer* was obtained at Delacroix Island, St. Bernard Parish, Louisiana, a locality said to have exceedingly brackish waters (Dr. George H. Bick, St. Mary's College, Notre Dame, Indiana); this adult male (TU 16170) is unique in having a mottled and blotched pattern. Another adult male (*spinifer*, TU 16071) was obtained in shallow water in Lake Pontchartrain at the mouth of Tchefuncta Creek; the salinity at the time of capture was recorded as 1.7 (datum from Dr. Royal D. Suttkus, Tulane University), indicating only slightly brackish water. Two *spinifer* (USNM 100409-10) and one *muticus* (USNM 100406) were taken at Berwick Bay, near Morgan City, St. Mary's Parish, Louisiana; the waters at this locality are probably brackish. The tolerance of brackish waters doubtless facilitates the dispersal of these turtles along coastal marshes and swamps, and into adjacent drainage systems. The greater number of records in the literature pertaining to *ferox* suggest that this species may be more tolerant of brackish and marine waters than are *spinifer* or *muticus*.

In summary, *T. ferox* occurs in all fresh-water habitats, but chiefly in lentic habitats in the northern part of its range where it and *T. s. asper* are sympatric. *T. ferox* possibly is more tolerant of brackish and marine waters than are the subspecies of *spinifer* and *muticus*.

The subspecies of *T. spinifer* occur in all fresh-water habitats. In the southern part of the geographic range, which overlaps that of *T. ferox, T. s. asper* occurs principally in running-water habitats. *T. s. pallidus* and *T. s. asper* are tolerant of brackish-water habitats. *T. s. guadalupensis,* known at present only from rivers and streams, occurs principally in river systems that drain the Edward's Plateau of southcentral Texas. *T. ater* is confined to crystal clear ponds in central Coahuila.

The subspecies *muticus* occurs in large rivers and streams throughout its geographic range, but is known from lakes and impoundments principally in the southern part of its range (the northernmost record is from Reelfoot Lake, Obion County, Tennessee); there is only one record of *muticus* from a small, shallow, headwater creek (Reno County, Kansas), and only one from a lentic habitat (Meredosia Bay, Illinois) in the northern part of its range. *T. muticus calvatus* is known at present only from rivers and streams.

The seemingly greater restriction of *muticus* to running-water habitats suggests less vagility than in *spinifer* (Netting, 1944:86).

Size and coloration are adaptations to habitat. Soft-shelled turtles of large size are best adapted to mesic, essentially continuous swampy or marshy habitats, whereas small size is an adaptation to less continuous, semi-isolated habitats. A turtle of the maximum size attained by *ferox* in the habitat of *emoryi* would, in a general way, probably be more conspicuous and exposed to its enemies, both in the aquatic environment and during overland excursions; perhaps the kind and amount of food would be insufficient. In any event, small size is correlated with the more arid habitats of the southwest, and large size with mesic ones in the southeast. *T. ferox,* the largest species, and the smallest population of *T. spinifer* (resembling *muticus*) both occur in the southernmost part of the range of the genus. This situation does not support the corollary of Bergmann's Rule, that pertains to some groups of terrestrial reptiles, in which those subspecies occurring farther north, or in cooler climates during their season of activity, tend to be smaller.

Within the species *spinifer,* the *emoryi* group of subspecies are pallid having whitish dots on the carapace and lack extensive black pigmentation; these features seem to confer protective coloration on the inhabitants of arid, essentially sandy or muddy habitats having sluggish, turbid waters, whereas the more contrasting patterns of the *spinifer* group of subspecies eastward seem more suited to existence in clearer, swifter waters.

The occurrence of the two clines, *spinifer-hartwegi* and *pallidus-guadalupensis,* in the species *spinifer* are notable in that the former occurs mostly in one large continuous drainage system, that of the Mississippi, and shows no sharp break in the one character distinguishing the two subspecies whereas populations composing the *pallidus-guadalupensis* cline are separated into several river drainages, and show a relatively sharp break in several characters at the Brazos-Colorado river divide. This situation seemingly supports the thesis that clines are maintained by some sort of parallel gradient in ecological or geological conditions. It is notable that streams draining the Edward's Plateau (inhabited by *guadalupensis*) differ in quantity (more) and quality (especially CO_3^{--}, Ca^{++}, and Mg^{++} ions) of their solutes, and probably pH (higher) from those farther east (Hubbs, 1957:102). The gross difference in habitats mentioned above (sandy, turbid, sluggish streams in the west *vs.* clear, swift streams in the east) may affect the differentiation recognizable in the *spinifer-hartwegi* cline.

Daily and Seasonal Activity

Diurnal Habits

Softshells bask on débris in the water or on banks close to the water; basking presumably raises the bodily temperature. In general in the southeastern and southwestern United States, I have seen softshells basking only rarely but once saw six at one time close together on logs in Bowie Creek, Hattiesburg, Mississippi (species undetermined). Surface (1908:122) saw *spinifer* in rows on rocks or logs in tributaries of the Ohio River. Duellman and Schwartz (1958:271-72) stated that *ferox* basks on banks or beds of aquatic vegetation. Deckert (1918:31) mentioned large *ferox* "sunning in shallow water at edge of pond." Minton (1944:447) wrote that *muticus* and *spinifer* sun on steep mud banks (Wabash River). Cahn (1937:180) stated that *muticus* (in Illinois) basks on banks at the water's edge but seldom on logs, and suggests that *muticus* is less prone to leave the water than *spinifer.* According to Carr (1952:438), *muticus* never basks on logs or rocks. In Ohio, Conant (1951:159) mentioned *spinifer* as occasionally basking upon a log or rock, or sometimes on steep clay banks of streams. On banks, quick escape is facilitated by directing the head toward the water, thus eliminating the time that it would take to turn around on land (Conant, *loc. cit.*; Newman, 1906:129). Evermann and Clark (1920:593) mentioned *spinifer* as basking on sandy or grassy shores, and large boulders. Muller (1921:181) wrote that *muticus* basks four to ten feet from the water's edge on gently sloping sand and mud shores of small islands in the Mississippi River (near Fairport, Iowa). Muller stated that basking usually occurs in the morning, up until 2 p. m., and that beaches with a northern exposure were preferred; he observed 37 turtles within a 50-foot stretch of beach. In captivity, hatchlings bask on wire-mesh supports.

I have frequently observed softshells floating at the surface of the water, a habit previously mentioned by Surface (1908:122) and Pope (1949:305, 311). Individuals of *Pseudemys* and, to a lesser extent, *Graptemys* also float at the surface; those kinds of turtles and softshells at least, often appear at the surface of the water, seemingly as a result of an inquisitiveness, following repeated disturbances that cause submergence.

Newman (1906:131) described the active pursuit of food: "They crawl or swim along the bottom, thrusting their snouts under stones and into masses of aquatic vegetation, occasionally snapping up a crayfish or larva that they have succeeded in dislodging. They do not tear up their food, but swallow it whole, using the forefeet to assist in forcing it down." Surface (1908:123) suggested that softshells may feed "upon insects which may be found floating on the water," and I have had captives take insects from the surface of the water. Carr (1940:107) also wrote that *ferox* and numerous gars in the Tamiami Canal, often at the mouths of the tributary ditches, snap at each other furiously as floating bits of food are washed in from the Everglades. Another habit that has been mentioned as an aid in acquiring food (Breckenridge, 1944:186; Conant, 1951: 156; Hudson, 1942:101) is burrowing just below the surface in a soft bottom in shallow water, to ambush passing fish, or other food. Presumably all kinds of softshells do this in both shallow and deep water of lakes or rivers having a suitable substrate; *spinifer* and *muticus* have been reported to burrow in shallow waters (no observations in deep water) by Agassiz (1857:333), Cahn (1937:180, 189), Conant (1951:159) and Weed (1923:48). Marchand (*in* Carr, 1952:417-19) noted that *ferox* burrows in deep water, and mentioned that in areas of bare white sand a group of fish invariably surrounds them, and one can locate buried softshells by observing these particular schools of fish. No mention was made of the turtles attempting to catch the fish. Other associations of soft-shelled turtles and fish have been described. Kirtland (*in* DeKay, 1842:7) observed several large bass that closely followed large numbers of turtles floating at the surface. Newman (1906:131) reported the observations of fishermen in Lake Maxinkuckee that large-mouth black bass stay not far away from swimming softshells; the same author also mentioned the observations of Jacob Reighard, who suggested that bass may be feeding upon minnows that he noticed following softshells. Seemingly some sort of commensalistic relationship exists whereby fish acquire food that is dislodged by grubbing and scurrying of softshells. Probably food is pursued on occasion from a buried position, but this habit probably is not executed specifically for obtaining food. Newman (*op. cit.*:129) was of the opinion that burrowing in shallow water is a habit to facilitate "warming up."

Marchand (*loc. cit.*) also wrote of other notable underwater observations on *ferox* in Florida. He commented on this turtle's inquisitiveness in deep water and unconcern upon being touched or even upon being handled to some degree. Calf-deep in soft mud, he noted a turtle that "emerged from the mud of the bottom, headed up toward shore, circled, and when about three feet above the bottom dived suddenly and completely disappeared." Marchand wrote that some areas on the bottom (Crystal Springs), which are rooted up by the burrowing of softshells, are bare and soft, and assume a characteristic, easily recognized, appearance.

Cahn (1937:180, 189) stated that the burrowing process consists of "flipping" the loose sand or silt over the back, whereas Conant (1951:159) described the process as a rapid lateral movement of the body. My observations of captives agree essentially with Conant's observations. The initial movement, directed at a slight angle, is principally with the forelegs although complemented by lateral movements of the body. When the turtle is approximately half buried, it makes rapid lateral movements of the body, which completely bury the turtle and orient its body in a horizontal position.

Behavior and Adaptations

Some characteristics of softshells that are often mentioned in the literature are: extreme shyness or wariness, ferociousness as captives, dazzling speed and agility on land and in water, and great dependence on aquatic environment. Certainly they are wary; and this wariness may account, in part, for the scarcity of observations of basking, and statements attesting to their great speed on land. To my mind, their reported ferociousness and savage disposition as captives is overrated; of the many softshells that I have collected, only a few attempted to bite. The extensibility of their long neck does warrant more careful handling than needs to be employed with other species. Holbrook (*in* Hay, 1892:145) even wrote that they "will sometime leap up and give a loud hiss," and Newman (1906:130) wrote that "they hiss violently and thrust out the head." Wright and Funkhouser (1915:120) reported a captive *ferox* that "could jump forward practically its own length." I have been bitten by individuals of *Kinosternon, Sternothaerus, Pseudemys* and *Graptemys,* and cannot support the contention that softshells are more prone to bite than those species, a view shared by LeConte (*in* DeKay 1842:7); many softshells on initial capture will tend to withdraw the head completely for a short time. Newman (*loc. cit.*) also wrote that recently captured specimens exude a thick, yellow, semi-fluid resembling yolk of an egg from the inguinal glands; the substance, however, is odorless but "undoubtedly homologous with the emission of the inguinal glands of the musk and snapping tortoises." Perhaps there is a difference in aggressiveness associated with geographic location, the age of the turtle or individual temperament.

Smith (1956:159), referring to *muticus,* wrote that they are the best swimmers of all fresh water turtles, and perhaps of any turtles. Corresponding statements of other authors attesting to their speed and agility (including *spinifer* and *ferox*) in water and on land are based principally on the published comments of Muller (1921:181), who observed that females disturbed while laying eggs "about fifty feet from water . . . covered the distance faster than a man can run." Cahn (1937:180) also stated that *muticus* on a "level, unobstructed sand beach . . . can outrun a man," and (*op. cit.*:181) can "capture fish with ease"; Cahn supported the latter statement by relating his observation of a *muticus* that captured a small brook trout in a large tank. Smith (*op. cit.*:162) wrote that *spinifer* is "said to overtake bass." Doubtless they are good swimmers and they do scurry rapidly on land.

Published statements relating to the strictly aquatic existence of softshells especially *muticus,* are based on recognition of "its drastic adaptations to aquatic existence" (Carr, 1952:428); these adaptations presumably include pharyngeal respiration and the marked depression of body form. Pharyngeal respiration was demonstrated for *muticus* and *spinifer* (Gage, 1884; Gage and Gage, 1886), and was considered the prinicipal type of aquatic respiration (some dermal and some cloacal) in *Trionyx spinifer asper* by Dunson (1960). Cloacal bursae (anal respiration) are lacking in trionychids (Smith and James, 1955:88). Accessory pharyngeal respiration is meaningful in light of the information furnished by Agassiz (1857:282-83), who found that *Trionyx* has a smaller lung capacity (weight of body in ounces/capacity of lungs in cubic inches = 16.9) than do some other genera (*Pseudemys,* 2.8; *Testudo,* 2.7; *Terrapene,* 1.1); corresponding values for more aquatic species were *Chelydra,* 9.3 and *Kinosternon,* 16.0. Cahn (1937:181), however, wrote that he has demonstrated pharyngeal respiration in individuals of *Pseudemys, Chrysemys* and *Sternothaerus,* and Allen and Neill (1950:13) suggested that it occurs in *Macroclemys.* More conclusive data are required to detect a positive correlation between small lung capacity, pharyngeal respiration, and degree of restriction to an aquatic habitat.

The depressed, soft-margined carapace of softshells has been mentioned as an adaptation to facilitate burrowing in soft sand or mud, and more suited for concealment than for speed in aquatic locomotion (Carr, 1952:429; Smith, 1956:162). Nielson (1951:264-65), commented that in various lotic invertebrates, dorsoventral flattening of the body was no commoner than in lentic invertebrates; he wrote that a dorsoventral flattening is a disadvantage to an animal in a strong current and is an adaptation "probably . . . not to withstand the current directly, but to avoid it by seeking shelter in narrow crevices." Probably another aid to concealment, mentioned by Williams and McDowell (1952:272), is the plastral hinge.

Concealment of softshells is not enhanced by growths of algae on the carapace. Proctor (1958:637-38) reported that the common, epizoöphytic alga of chelonians, *Basicladia,* has never been reported from *Trionyx;* the same author recorded a large amount of filamentous algae, principally *Stigeoclonium,* but the algae could be easily wiped from the turtle, and Vinyard (1955:64) recorded an alga, *Dermatophyton radians,* attached to the skin of the legs of *Trionyx.* I noted a small patch of greenish scum growing near the insertion of the neck on a softshell (*spinifer* from Lake Texoma); cursory examination by Dr. R. H. Thompson, disclosed one of the colonial ciliate protozoans (resembling *Opercularia*) with enmeshed green or blue-green algae. Evermann and Clark (1920:592) mention a *spinifer* from Lake Maxinkuckee, Indiana, having a growth of *Opercularia,* covering the plastron.

Movement

The reported proclivity of softshells for a strictly aquatic existence has been over-emphasized; they are no more confined to aquatic habitats than some chelydrids (including kinosternids). In fact, there is a general parallel in habits between members of the two families, namely, a tendency toward a bottom-dwelling existence, and a burrowing habit. The alligator snapping turtle (*Macroclemys*) is probably the most aquatic fresh-water turtle in the United States. The common snapping turtle and some kinosternids are known to migrate overland. Kinosternids and trionychids bask frequently, and trionychids have been observed moving overland. Cox (1894:50) reported a *spinifer* attempting to climb a narrowly-stepped, 12-foot dam on Mud Creek at Ravenna, Nebraska; the turtle failed after repeated struggles, once reaching a height four inches shy of the brim before tumbling back into the water. Duellman and Schwartz (1958:271) commented that adults of *ferox* are often seen on roads bordering canals, and informants have told me verbally of similar observations. Conant (1930:61) reported an individual of *ferox* that was ". . . walking across the main street in Venice [Sarasota County, Florida]." Softshells will travel overland in search for suitable nesting sites; Newman (1906:130) wrote that *spinifer* will climb "steep railwav embankments with considerable ease, in order to reach a sand pit some fifty yards from the water."

From an analysis of species-composition of large reservoirs and lakes and their adjacent smaller ponds in southern Illinois, Cagle (1942:162) concluded that softshells "travel overland far less often than do . . ." other species, but that they are "probably the first to move as the water level falls." On the basis of further observations in the same region, Cagle (1944:15) wrote that softshells rarely move overland, and once trapped in a pool of water, they bury themselves and remain there. He related instances of several individuals having been dug from dried mud where the last remnants of a water pool had evaporated and he concluded that the home range is probably confined to one body of water. That fluctuations in water level affect the movement of softshells is suggested by Mr. William E. Brode's comment that a commercial fisherman trapped numerous softshells in the Pearl River, south of Monticello, Mississippi, in unbaited hoop-nets in late May and June when the water level was receding after heavy rains.

The meager data available concerning the aquatic movements of softshells indicate that individuals wander but little. Breckenridge

(1955:6, table 1) found that among 30 recaptured turtles that had been marked, the greatest distance traveled was 600 yards over a two-year interval; after a three-month interval one originally captured 30 miles distant, moved only 200 yards. The statement of a professional turtle trapper mentioned by Breckenridge (*loc. cit.*) and data previously presented (see page 436), to the effect that overtrapping results in increasingly diminished returns, tends to support the idea that there is little aquatic movement in soft-shelled turtles.

Breckenridge (*loc cit.*) mentioned methods of marking softshells and found that notching the edge of the carapace with a leather punch was satisfactory; the notches healed but were discernible as shallow sinuses. The same author mentioned a tattooing device (mentioned also by Cagle, 1939:171), but no turtles so marked were ever recognized as recovered. Tagging with a radioactive isotope and detection with suitable instruments should prove applicable to turtles (see Karlstrom, 1957).

Nocturnal Habits

Anderson (1958:212) wrote that hatchlings (*muticus*) leave nests within the first three hours after sunset, and are active on the surface of the sand at night. Muller (1921:183) reported hatchlings (*muticus*) leaving nests at night or early in the morning. Lagler (1954) stated that *spinifer* is nocturnal. To my knowledge there are no other published statements concerning nocturnal activity of soft-shelled turtles. I have noted them at night on only four different occasions. In two instances (Clear Fork Brazos River, Texas, and Lake Concordia, Louisiana), the turtles were resting immediately below the surface of the water on submerged branches, as one would expect *Pseudemys* and *Graptemys* to do. Another individual was seen swimming near the surface (Ocmulgee River, 1½ mi. S Jacksonville, Georgia); this observation possibly represents nocturnal activity, or inquisitiveness owing to the disturbances caused by the motor of the boat and/or our head lights. A final observation tends to support the view of nocturnal habits. My field notes record at least four softshells collected by hand, and a few other seen in a shallow (approximately four feet deep), quiet, clear water side channel of the White River (Cotter, Arkansas); the turtles were seen resting and slowly moving on the bottom or swimming.

Seasonal Occurrence

The length of the season of activity increases with decrease in latitude. Aquatic species in general have longer periods of activity than terrestrial species at the same northern temperate latitudes. The southernmost populations of all species of softshells may be active throughout the year, assuming temperature to be the limiting factor.

There are few published statements relative to the length of the annual period of activity; all records refer to *spinifer*. In Lake Maxinkuckee, northern Indiana, Newman (1906:128) wrote that individuals were first seen in early April on the lake shore in a weak condition with neck and legs extended, and were easily captured. Lesueur (1827:262) wrote that *spinifer* in Indiana appears toward the end of April. Observations of Evermann and Clark (1920:592) in Lake Maxinkuckee, and Butler (1894:224) in east central Indiana concurred in finding that of all kinds of turtles there, softshells appeared last in spring and disappeared first in fall. Evermann and Clark found small softshells, benumbed or dead, along the shore as early as March 18 and also late in fall. The earliest observation for large softshells was April 29, and the latest was September 7; Butler found that these turtles rarely appear before April 15 and sometimes not until May 1. Cahn (1937:191) stated that softshells in Illinois hibernate toward the end of October and emerge in May or the latter part of April; the same author mentioned that in southern Illinois the species might remain sluggishly active all winter. In Ohio, Conant (1951:160) wrote that individuals were collected every month from March to October, and one was even taken in December, 1929, in northwestern Ohio. Wright (1919:8) mentioned observing softshells on April 20 and September 20 (presumably these were the earliest and latest observations of them) in Monroe and Wayne counties, New York. Blatchley (1891:34) listed dates of early and late activity as March 19 and December 11 for Vigo County, Indiana. Webster (1936:22) recorded the earliest and latest dates of collection of *spinifer* in central Oklahoma as June 10 and November 8.

Moore and Rigney (1942:80) found an individual of *muticus* under six inches of ice in water about one foot deep on January 31, 1940 (Cimarron River, Payne County, Oklahoma).

The published information suggests that the length of the normal annual period of activity of *spinifer* in latitudes of about 40° and 43° is approximately five months, from April into September, depending upon the weather. There are numerous published statements to the effect that the period of hibernation is passed under a shallow covering of mud in deep water. Evermann and Clark (*op. cit.*:

593) found a softshell (presumably in a quiescent state) on September 6 that was "buried up to its eyes in mud at the edge of Lost Lake." Softshells possibly hibernate in shallow water or in soft mud flats. Conant (*loc. cit.*) found that captives would not hibernate in a pond in a zoo having a bottom of leaves.

Food Habits

Previous authors, most of whom allude to published statements preceding their own, characterize soft-shelled turtles as carnivorous and mention such food items as crawfish, insects, worms, snails, clams, frogs, tadpoles, fish, and occasional vegetable matter. Stockwell (1878:403) wrote that the relative lengths of portions of the digestive tract indicate "a purely carnivorous diet."

In an examination of the contents of 11 stomachs of *spinifer* from Michigan, Lagler (1943:304) found that crawfish (47%) and insects (52%), principally burrowing mayfly naiads (*Hexagenia*), and dragonfly naiads, comprised the bulk of the diet with cryptogams, vegetable débris, snails and fish remains present in small amounts. Breckenridge (1944:186) wrote that 18 specimens of *spinifer* in Minnesota contained 44 per cent crawfish, 29 per cent aquatic insects, 8 per cent fish, and 19 per cent unidentified material. Surface (1908:123) found crawfish in the only two stomachs of specimens he examined from Pennsylvania. Penn (1950) summarized the results of those authors, and estimated that crawfishes comprised 58 per cent (46% by volume) of the diet of softshells. In Indiana, three stomachs examined by Newman (1906:131) in late June contained: 1) nine crawfish, 2) four crawfish, 22 dragonfly naiads, 3) nine dragonfly naiads, few plant buds. Neill (1951a:765) found crawfishes in the stomachs of five *spinifer* from the Savannah River, Georgia. Evermann and Clark (1920:595) wrote that *spinifer* in Lake Maxinkuckee feeds principally on crawfishes. Shockley (1949:257) mentioned bottom organisms and small fishes as food. Clark and Southall (1920:16) stated that "Its principal food, to judge from a few specimens examined, consists of crayfishes."

Cahn (1937:183) wrote that the food of *muticus* in Illinois consists principally of crawfish, fish, frogs, tadpoles, larger insect larvae and nymphs, and aquatic mollusks. The kinds of fish eaten were *Notropis heterolepis, N. spilopterus, N. hudsonius, Lepomis machrochirus, Morone chrysops, Perca flavescens, Catostomus commersonnii,* and *Hypentelium nigricans;* Cahn (*loc. cit.*) also stated that the mollusks eaten by *muticus* are both gastropods and small, thin-shelled bivalves. In regard to the feeding habits of *spinifer* in Illinois, Cahn *op. cit.*:193) listed the following items in decreasing order of abundance as revealed by examinations of stomachs: crawfish, minnows, fry of larger fish, frogs, tadpoles, earthworms, insects (often beetles), and mollusca (*Pisidium, Viviparus,* planorbids). The kinds of fish mentioned were: *Notropis heterodon, N. heterolepis, N. hudsonius, Catostomus commersonnii, Lepomis humilis, L. macrochirus, Semotilus atromaculatus, Notemigonus crysoleucas, Umbra limi,* and *Micropterus salmoides.* Cahn (*loc. cit.*) also found the remains of a six-inch brook trout (*Salvelinus*) in the stomach of a 13-inch *spinifer* from Wisconsin.

Agassiz (1857:399) found larvae of neuropterous insects in the stomach of one specimen of *muticus*, and fragments of *Anodonta* and *Paludina* (= *Campeloma*) in the stomach of one *ferox*. The expanded crushing surfaces of the jaws in some large individuals of *ferox* may be an adaptation to mollusc-feeding (Schmidt and Inger, 1957:36). Surface (1908:123) found *spinifer* to have fragments of beetles in one of two specimens examined, and large quantities of corn in another from Ohio. Webb and Legler (1960:27) reported 23 chrysomelid beetle larvae (*Donacia*) in one specimen of *T. ater*. Evermann and Clark (1920:595) reported several *spinifer* taken on hooks baited with grasshoppers in water 14 feet deep in Lake Maxinkuckee, Indiana. Hay (1892:144) wrote of *muticus* that "If there are potatoes growing near the water the turtles find their way to them and devour the stems, of which they are very fond." Wright and Funkhouser (1915:123) stated that young *ferox* in the Okefinokee Swamp feed on fish and frogs, and according to the natives, larger specimens take waterfowl, a statement that Smith (1956:159) was probably reiterating when he mentioned that the diet included "perhaps young birds." Parker (1939:88) wrote that of two *spinifer* from Reelfoot Lake, Tennessee, one contained coleopteran remains, and the other an aquatic beetle and two large tipulid larvae. Wied-Neuwied (1865:54) wrote that Lesueur found worms, snails, remains of *Paludina* (= *Campeloma*), fruits and even hard nuts in stomachs of *muticus*.

Holbrook (*in* Hay, 1892:145) mentioned that *spinifer* feeds on fish and such reptiles as it can secure. There are no published statements known to me that report reptiles in the diet of American softshells. Carr (1952:425) erroneously cited Strecker (1927:9) and attributed "a young lined snake" to the diet of *T. s. emoryi;* Strecker, however, referred to *Kinosternon flavescens*. In conjunction with raising softshells on turtle farms, Mitsukuri (1905:261) mentioned that first and second year-old turtles (*Trionyx sinensis*) must be transferred to separate ponds or they will be eaten by adults; perhaps corresponding cannibalistic tendencies exist in confined, natural habitats in American softshells.

Captives eat essentially the same things that free-living individuals do, plus scraps of meat (Strecker, 1927:9; Gloyd, 1928:135; Pope, 1949; Conant, 1951:156, 160). Lagler (1943:303) mentioned a young *spinifer* that fed on water fleas (*Daphnia*) and canned fish. Conant (*op. cit.*:160) wrote that no captive was observed to take vegetable matter.

Food, mostly in intestines, of two adult females of *T. s. emoryi* collected on June 12-14, 1959, from the Río Grande at Lajitas, Brewster County, Texas, was examined. One female, KU 51961, contained little food and mostly plant fragments; because the stomach or intestine was not full of plant fragments, this food probably was ingested incidentally to the few insects present. Another female, KU 51955, contained insects, which were identified by Dr. George W. Byers, Department of Entomology, University of Kansas, as follows: 1) Coleoptera, Dryopidae, genus *Helichus*, most numerous, 350 to 400 individuals; 2) Coleoptera, Scarabaeidae, genus *Phyllophaga*, one individual; 3) Odonata, Coenagrionidae, fragments, probably one individual; 4) Hymenoptera, Sphecidae, subfamily Bembicinae, one individual; 5) Ephemeroptera; fragments of naiad; and 6) a few plant seeds, pieces of slender roots, weed stems and a couple of fragments of tree bark. The scarab and wasp probably fell into the water and were eaten.

Food from the digestive tracts of 11 specimens of *T. m. muticus* from the

TABLE 6. KINDS OF INSECTS FOUND IN STOMACHS AND INTESTINES OF 11 SPECIMENS OF TRIONYX M. MUTICUS (EIGHT ADULT MALES AND THREE IMMATURE FEMALES, 9.0 TO 12.5 CM. IN PLASTRAL LENGTH) FROM DOUGLAS COUNTY, KANSAS. FREQUENCY OF OCCURRENCE (APPROXIMATE NUMBER OF INDIVIDUAL INSECTS/NUMBER OF STOMACHS IN WHICH FOUND) IS GIVEN FOR EACH ITEM LISTED. FRAGMENTS OF INSECTS REPRESENT ADULTS UNLESS OTHERWISE NOTED.

FOOD ITEM	Frequency
Orthoptera	
Locustidae	1
Ephemeroptera	
Unknown (naiad)	1
Odonata	
Anisoptera (naiad)	3/3
Zygoptera (naiad)	4/2
Plecoptera	
Unknown (naiad)	2/1
Homoptera	
Cicadellidae	20/7
Hemiptera	
Lygaeidae	1
Neuroptera	
Corydalidae (*Corydalis* larva)	1
Trichoptera	
Hydropsychidae? (incl. 18 larvae and 4 pupae)	23/9
Unknown (incl. 1 larva)	4/4
Lepidoptera	
Noctuidae? (larvae)	2/1
Pyralidoidea (larva)	1
Unknown	1
Coleoptera	
Carabidae (incl. 1 larva)	3/3
Cerambycidae?	1
Chrysomelidae	1
Cicindelidae (larva)	1
Elateridae (larva)	1
Hydrophilidae? (larvae)	4/2
Scarabaeidae (incl. *Phyllophaga*)	9/6
Diptera	
Anthomyiidae	1
Asilidae	1
Bibionidae (*Bibio*)	5/2
Calliphoridae (puparium)	1
Empididae	1
Mycetophilidae	1
Tipulidae (incl. *Tipula bicornis* and *T. triplex*?)	9/4
Unknown (5 muscoid, 3 acalyptrate, and 1 cyclorrhaphous types)	9/4
Hymenoptera	
Apoidea	1
Formicidae (incl. *Camponotus*)	11/4
Ichneumonidae (one questionable)	4/3
Tenthredinidae	1
Unknown (small wasps)	3/2

Kansas River at Lawrence, Douglas County, Kansas, were examined (Table 6). The turtles (KU 55296-306, eight adult males and three immature females, ranging in plastral length from 9.0 to 12.5 cm.) were collected in June, 1958, by Mr. Robert R. Patterson. All turtles were caught on hook and line in a period of about four or five hours at dusk. Patterson frequently fished below the bridge at Lawrence and observed that heads of softshells were often seen there about dusk and that the turtles seemed to prefer a rather shallow, quiet-water area of swirls and eddies for feeding. The stomachs, and to a lesser degree, the intestines, were nearly full. Some turtles contained plant fragments, principally elm seeds. The kinds of food in this sample were also identified by Dr. Byers and were mostly insects, the most frequent item being trichopterans; many of the insects eaten undoubtedly fell into the water. The remains of spiders were found in four stomachs and crawfish fragments in five.

Stomachs of two adults of *muticus* from Lake Texoma, Oklahoma, were opened. The stomach of one (OU 27593) was full of naiads of the burrowing mayfly *Hexagenia;* that of the other female (OU 27594) contained exoskeletal remains of crawfish. The two specimens were drowned in gill nets between the hours of 11 a. m. and 7 p. m., on July 10, 1954; the intact condition of the mayfly naiads indicated recent feeding.

The species of American softshells are mainly carnivorous. The presence of vegetable matter (mentioned in previous paragraphs) in the digestive tracts of many specimens and True's statement (1893:152) that soft-shelled turtles include a variety of vegetable matter in their food indicates omnivorous habits. Duellman and Schwartz (1958:272) stated that *ferox* is omnivorous and Carr (1952:430) made a similar statement for *spinifer*. The diet seems to be determined by the food supply available, which may vary seasonally or with adverse conditions such as flooding; under normal environmental conditions, however, vegetable matter probably is ingested incidentally to other food. There is no indication of a preference in food habits according to species and subspecies. Most of the food seems to be obtained by active foraging that is triggered primarily by movement of the prey; the sense of smell is probably secondary.

Reproduction

Size of males at Sexual Maturity

Elsewhere (1956:121) I have shown that males of *spinifer* from Lake Texoma, Oklahoma, and scattered localities in Texas and Louisiana are sexually mature when they reach a plastral length of 9.0-10.0 centimeters. Adult males have distinct, convoluted, nonpigmented vasa deferentia and elongate testes, the maximal measurements of which are about 10 by 30 millimeters. Testes of hatchlings are approximately 4.0 by 0.4 millimeters (TU 13698.12, plastral length 3.2 cm., measured with ocular micrometer). I am not aware of seasonal changes in size of the testes.

In reading the discussion that follows, it is well to remember that males having the cloaca extending beyond the posterior edge of the carapace are regarded as sexually mature. As an indication of geographic variation in *spinifer,* I have listed the measurements of the 10 smallest males for only those subspecies of which there are numerous records (Table 7). Corresponding data for *T. muticus muticus* are also listed for comparison.

The data indicate that the size at which sexual maturity is attained in *emoryi* (about 8.0-9.0 cm.) is less than in any other subspecies of *T. spinifer* (about 9.0-10.0 cm.), and, more importantly, corresponds to that of *T. m. muticus.* Although the mean for *T. s. spinifer* is slightly less than in the remaining subspecies, I doubt that there is any significant difference according to subspecies in the size at which sexual maturity is attained in the subspecies *spinifer, hartwegi, asper, pallidus* and *guadalupensis.* The corresponding size in *T. m. muticus* and *T. s. emoryi* heightens the morphological resemblance between these forms. The only sexually mature male of *T. ater,* which morphologically resembles *emoryi* and *muticus,* is 9.5 centimeters in plastral length. I do not know the size at which *T. ferox* attains sexual maturity. The smallest sexually mature individual examined by me was 12.0 centimeters; probably *ferox* attains sexual maturity at a larger size than *spinifer* or *muticus.* The relative size of attainment of sexual maturity in *ferox, spinifer,* and *muticus* corresponds to the maximum size of the three species; *ferox* is the largest species and *muticus* is the smallest (Table 2).

TABLE 7. SIZE AT SEXUAL MATURITY OF THE 10 SMALLEST MALES OF T. M. MUTICUS AND SELECTED SUBSPECIES OF T. SPINIFER. THE EXTREMES PRECEDE THE MEAN (IN PARENTHESES).

SPECIES AND SUBSPECIES	Plastral length (cm.)
T. s. spinifer	8.8-10.3 (9.6)
T. s. hartwegi	9.6–10.5 (10.2)
T. s. pallidus	9.1–11.2 (10.5)
T. s. guadalupensis	9.3–10.8 (10.1)
T. s. emoryi	8.2–9.0 (8.8)
T. m. muticus	8.2–9.2 (8.7)

Size of Females at Sexual Maturity

Breckenridge (1955:6) wrote that the development of the mottled pattern "undoubtedly indicates a stage in the attainment of sexual maturity"; I have mentioned (1956:121) that the mottled pattern is apparent on females before sexual maturity is attained. To my knowledge females have no external characters which appear at the time of attainment of sexual maturity.

Sexually mature individuals of *ferox* have been described in various terms: 31¼ pounds (Goff and Goff, 1935:156); six pounds, lengths of carapace 10½ and 13 inches (Hamilton, 1947:209); greatest width of head 3½ inches (Wright and Funkhouser, 1915: 120). A 10½ inch carapace presumably represents the smallest turtle and corresponds to a plastron approximately 22.0 centimeters in length. There is no other information available concerning size at sexual maturity in *T. ferox.*

There is little published information concerning the size at sexual maturity in *T. spinifer.* Cahn (1937:193) wrote that *spinifer* in Illinois "must attain a carapace length of about 24 centimeters [plastral length approximately 18.0 cm.] before the females become sexually mature"; this statement is the basis for Smith's mentioning a length of 9½ inches (1956:162). Evermann and Clark (1920: 595) recorded the lengths of carapace of some females (presumably all adult) from Lake Maxinkuckee, Indiana, as 11, 11¾, 12½, and 13 inches; the smallest measurement corresponds to a plastral length of approximately 21.0 centimeters.

The data concerning reproduction presented in succeeding paragraphs is based principally upon examinations of turtles in the TU collections; I am indebted to Dr. Fred R. Cagle for permission to dissect these turtles. Females are regarded as sexually mature when they have oviducal eggs or corpora lutea or ovarian follicles exceeding 15 millimeters in diameter. Hatchlings of *spinifer* have ovaries that measure approximately 6.0 x 0.3 millimeters, and straight oviducts 0.2 millimeters in width (TU 5988, plastral length 3.5 cm. measured with ocular micrometer). In the size at which sexual maturity is attained there seems to be much individual variation as well as geographic variation.

Females of *T. s. emoryi* from the Río Grande in the Big Bend region of Texas are sexually mature when the plastron is approximately 16.0 centimeters (16.2 cm., KU 51960), and are the smallest adult females of *spinifer* that I have seen; these females are representative of the population from which the smallest adult males of *spinifer* are known and which is unique in showing sexual differences in coloration. A female (TU 3697), having a plastral length of 16.0 centimeters, which was obtained in the Río Grande near Eagle Pass, Texas, in mid-July, is immature; the ovaries are compact having the largest follicles 2.5 millimeters in diameter, and the oviduct is wrinkled and convoluted but only six millimeters wide. Of three females of *emoryi* from the Pecos River, Terrell County, Texas, having plastrons 17.4, 18.3 and 18.8 centimeters in length and obtained on June 11, the largest and smallest are immature, and internally resemble TU 3697. TU 14453.2 (18.3 cm.) is sexually mature having large corpora lutea and enlarged ovarian follicles. KU 53754, from the Río Salado in central Coahuila, México, having corpora lutea and a plastral length of 20.3 centimeters, is sexually mature.

Females of *T. s. guadalupensis,* measuring 14.5, 15.7, 16.3, 16.5, 16.8, 17.0, 19.0, and 20.0 centimeters in plastral length and obtained from June to September, are immature. The female measuring 19.0 centimeters indicates the approach of sexual maturity in having swollen and convoluted oviducts seven to ten millimeters in width, but compact ovaries having the largest follicles 4.0 millimeters. The other *guadalupensis* whose measurements are given above have oviducts that do not exceed four millimeters in width, and ovarian follicles that do not exceed two millimeters in diameter. TU 10187, obtained in July, plastral length 19.5 centimeters, is sexually mature having corpora lutea and enlarged follicles. Two other *guadalupensis,* 21.5 and 22.0 centimeters (Pl. 12, top), having ovaries with enlarged ovarian follicles (the largest in one, only 11 mm.) are considered sexually mature.

Concerning the subspecies *pallidus,* females (all collected in June or July) measuring 15.7, 16.3, 17.3, 17.5, 18.7, 19.5, 20.8 and 21.3 centimeters in plastral length are immature having solid, compact ovaries with the largest follicles not exceeding two millimeters in diameter; oviducts are straight not exceeding three millimeters in greatest width, except those turtles measuring 17.3 and 21.3 centimeters in which the oviducts are swollen and convoluted and, respectively, five and eight millimeters in greatest width. The smallest sexually mature *pallidus* is 19.8 centimeters in length; recorded lengths of other adult females are 23.5, 26.8 and 30.5 centimeters.

Of especial interest are three large female *pallidus,* measuring 24.8, 27.5, and 28.0 centimeters, which appear to be immature; two of these (TU 13303-04) are from the Sabine River, collected in July, and the other specimen is without data (presumably from the Sabine River). The oviducts are large, swollen and convoluted, resembling those in sexually mature individuals. The ovaries, however, are relatively solid and compact having approximate measurements of 125 x 6 millimeters (TU 13303) and 85 x 10 millimeters (TU 13304), and follicles not exceeding five millimeters in diameter.

Females of *spinifer* from the lower Mississippi Valley of Louisiana having plastral lengths of 15.0, 15.5, 16.7, 17.5, 18.0, 19.5, 20.0, 20.4, and 20.8 centimeters are considered immature; the ovaries are compact and solid having follicles not exceeding three millimeters in diameter, and the oviducts, swollen and convoluted in the larger individuals, do not exceed six millimeters in width. The ovaries of the specimen 19.5 centimeters in length mentioned immediately above had been removed prior to my examination; the oviducts, however, were relatively straight and only five millimeters in width. Three females 23.0, 25.5, and 25.8 centimeters in length are sexually mature. TU 5518, measuring 21.5 centimeters in length and obtained in June, indicates the onset of sexual maturity in having large convoluted oviducts, but the ovaries are solid, compact, measuring 85 x 13 millimeters, and the largest follicles are only 4.5 millimeters. A larger turtle (TU 13080), 24.5 centimeters, obtained in July, has juvenal ovaries (largest follicles five mm.); the oviducts are enlarged and convoluted as in adult females.

Of two *T. s. asper* collected from the Escambia River in June and July, one 18.0 centimeters in plastral length is immature, whereas the other, 27.0 centimeters long, is adult. A female *T. s. hartwegi*, measuring 20.7 centimeters, is adult having enlarged follicles and corpora lutea (TTC 719, Pl. 36, bottom).

In summary, females of all subspecies of *spinifer*, except some *emoryi*, may be sexually mature when the plastron is 18.0 to 20.0 centimeters in length; probably all physiologically normal females are adult when 22.0 centimeters long. In general, females are sexually mature at a plastral length of approximately 20.0 centimeters, a measurement that corresponds to a length of carapace of approximately 28.0 centimeters or about 11 inches. Females representative of that population of *emoryi* inhabiting the Río Conchos and the Río Grande in the Big Bend region of Texas are adult when the plastron is approximately 16.0 centimeters in length, and are thus the smallest sexually mature females of the species *spinifer*. Oviducts are large (at least eight mm. in width, undistended), swollen and convoluted prior to the first ovulation.

Of interest are the large females (for example, TU 13303, plastral length 28.0 cm.) that seemingly have immature, relatively small, ovaries (the oviducts are large and convoluted as in adult females). Possibly such ovaries represent a regression and are in senile turtles, but I am inclined to believe that the development of these ovaries has been arrested probably owing to hormonal unbalance, and that they have never been functional.

The size of adult females of *T. ater* is unknown but probably approximates that of *T. spinifer* or is slightly less. Females of *ater* 15.5 and 17.2 centimeters in length are immature; the largest female, the holotype, is 18.3 centimeters in length, and was not dissected.

Females of *T. muticus* are sexually mature when smaller than *T. spinifer*. Two turtles, 13.8 and 14.0 centimeters in length, have large convoluted oviducts about 10 millimeters in width and ovarian follicles nine to twelve millimeters in diameter, and seem to be near sexual maturity. The smallest sexually mature female (subspecies *muticus*) is TU 14436, measuring 14.4 centimeters in plastral length and having oviducal eggs. Recorded lengths of other adult females are 16.3, 16.5, 17.2 (subspecies *muticus*), and 18.0 centimeters (subspecies *calvatus*). Two females having plastral lengths of 17.5 (subspecies *muticus*) and 16.0 centimeters (subspecies *calvatus*) seem sexually immature. These turtles collected in April and May have ovarian follicles not exceeding three millimeters in diameter.

Sexual Activity

Observations by Mitsukuri (1905:263), Conant (1951:160) and Legler (1955:98), constitute the extent of our knowledge concerning courtship and copulation. Legler observed a male *spinifer* and a female *muticus* in captivity; the male was the aggressor, following at the rear or above the female, and at times nipping at the anterior part of her carapace. During these movements, the posterior edge of the female's carapace was turned up slightly whereas that of the male was turned down; the turtles frequently surfaced to breathe. Occasionally the female followed the male. On the bottom the male crawled onto the female's carapace from the rear, remaining in a somewhat posterior position as described by Conant (*loc. cit.*), and seemingly not clasping the female with his feet. Copulation probably occurs in this position; Mitsukuri (*loc. cit.*) mentioned that copulation in *Trionyx sinensis* occurs at the surface of the water. The male remains in the coital position for approximately 15 seconds and then slowly drifts to one side and swims away. Legler observed five coital unions in one-half hour, each preceded by courting movements.

Legler's observations indicate that the courtship patterns of *muticus* and *spinifer* are similar, and that interspecific matings are possible. I have not noted any hybrid.

Risley (1933:689) mentioned differential movements of the sexes of *Sternothaerus odoratus* in conjunction with the breeding cycle. Such movements are revealed by trapping procedures that yield deviations from the expected 1:1 sex ratio. That differential sexual movements probably occur in *Trionyx* is indicated by my trapping 17 males in a group of 19 *spinifer* in hoop-nets in Lake Texoma in the period June 14-July 12, 1954. On June 24-26, 1959, a field party from the University of Kansas collected 15 softshells in hoop-nets at the mouth of the Río San Pedro, near Meoquí, Chihuahua; all turtles were males. On June 17-18, 1959, the same expedition trapped 11 males in a group of 13 turtles in the Río Conchos, near Ojinaga, Chihuahua. Earlier, June 12-14, 1959, 39 softshells were trapped in the Río Grande near Lajitas, Brewster County, Texas. Of these turtles, however, 19 were adult males and 20 were females; eight females were adult (sexually mature) all having oviducal eggs (Fig. 23). One of the two females from Ojinaga, KU 51174, is sexually mature (plastral length, 16.5 cm.) having oviducal eggs; the other is immature (plastral length, 8.0 cm.). The only softshell taken on June 21, 1959, 8 mi. N and 16 mi. W Ojinaga, KU 51173 (plastral length, 16.3 cm.) is a female having oviducal eggs. The two females from Lake Texoma are immature (plastral lengths, 9.8 and 12.4 cm.).

The results of trapping may indicate that females frequent shallow water for a short time before the period of deposition of eggs, but disperse to deep water after such periods or between them. The movements of immature females probably approximate those of adult males; the absence of immature females in the Meoquí series, and near absence (only one) in the Ojinaga series perhaps is due to fortuitous collecting methods or to slightly different diurnal movements between adult males and immature females. Females approaching sexual maturity and those sexually mature but not having oviducal eggs ready for deposition possibly remain relatively sedentary in deep water; such females possibly represent those absent in the 13.0-15.9 size group (Fig. 23). Certainly, factors other than those pertaining to egg deposition may cause mature egg-laden females to live in shallow water, or explain the deviations from the expected 1:1 ratio.

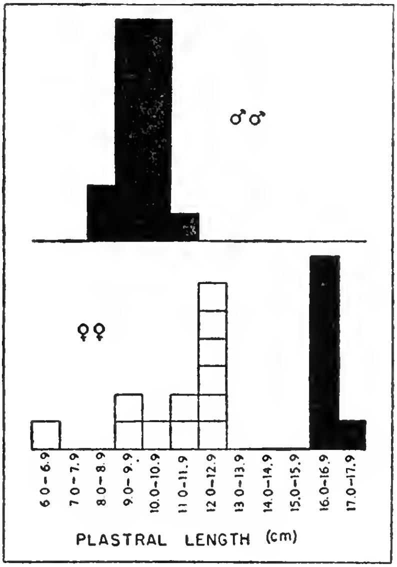


FIG. 23. Size distribution of 39 *Trionyx spinifer emoryi* (19 males and 20 females) collected in the period June 12 through June 14, 1959, from the Río Grande, near Lajitas, Brewster County, Texas. Solid squares represent sexually mature specimens. Females approaching sexual maturity or those not ready for egg deposition (13.0-15.9 cm. size group) are possibly sedentary in deep water.

One of the immature softshells (KU 51979, plastral length, 9.7 cm.) of the series from Lajitas is considered to be a female. It combines characteristics of both sexes. It resembles a male in having a carapace gritty to the touch, in having prominent white dots posteriorly and in not having a faint mottled and blotched pattern as do females of the same size. The postocular and postlabial markings are mostly yellow (female), but a small patch of the postocular stripe near the junction with the pale ventral coloration laterally is tinted with orange (male); the morphological characters and secondary sexual difference in coloration of this series of softshells has been mentioned on page 512. The tail is short and pyramidal resembling that of a female. Internally, there are a pair of ovaries and oviducts; KU 51979 is functionally a female. An over-production of androgens probably is responsible for the external masculine characteristics (orange color, gritty carapace and absence of mottling on carapace).

Deposition of Eggs

Concerning *T. ferox,* Wright and Funkhouser (1915:122-23) wrote that deposition of eggs occurred in June and July in the Okefinokee Swamp on the sandy parts of the islands or in sandy fields in places exposed to the direct rays of the sun. The same authors recorded a gravid female taken on June 22 (*op. cit.*:120), and a nest with eggs on June 26. Harper (1926:415) reported egg-laying in June in the Okefinokee Swamp. Goff and Goff (1935:156) found a female in search of a nesting site crawling toward a cleared area within a hammock at 11 a. m. on May 19, about 25 yards from the western shore of Lake Griffin, Florida. Carr (1940:107) stated that eggs in Florida "are laid from March to July 10. One individual laid her eggs on a block of ice which we had buried in the sand." Hamilton (1947:209) observed deposition of eggs near Fort Myers, Florida, in "a sandy roadbed slightly above the cypress swamp and ditch levels on either side of the road." . . . either in . . . "the ruts formed by cars or the slope of the roadbed"; dates of deposition of eggs recorded are March 30 at 11 a. m. in bright sun, and March 31 (from context, the date given as March 21 is considered an error) at 5 p. m. following a heavy rain. The daily temperatures at the time of Hamilton's observations "averaged 85° F., the first really warm spell of the season."

Eigenmann (1896:262) reported egg-laying of *spinifer* in sand and gravel in June and July at Turkey Lake (= Lake Wawasee), Indiana. A turtle was seen digging a nest on June 26, and fresh nests of eggs were found on June 27 and July 9. Hedrick and Holmes (1956:126) wrote that a clutch of eggs of *spinifer* in Minnesota was found about ten inches deep in sand about one foot from the river; a steep gravel bank was also cited as a favorite nesting site. Surface (1908:123) stated that eggs of *spinifer* in Pennsylvania are laid in May, and the young hatch in August. Gehlbach and Collette (1959:142) found eggs of *spinifer* on June 19 on a sand bank 15 feet from the edge of the Platte River in Nebraska. Breckenridge (1944:187) wrote that *spinifer* in Minnesota nests on sandy beaches from June 14 to July 6. Cahn (1937:193) stated that deposition of eggs in Illinois occurs in "June or early July: earlier in the southern part of the state, later in the northern portion." Force (1930:38) mentioned a gravid female from Oklahoma obtained on May 20. Evermann and Clark (1920:593) were of the opinion that *spinifer* began laying about mid-June and continued until perhaps late July at Lake Maxinkuckee, Indiana; a female opened on June 14 had oviducal eggs, and the first nest was found on June 18. Nests were usually at the edge of an abrupt ascent in sand; one nest was found in black, mucky soil (*op. cit.*:595). Newman (1906:128) wrote that *spinifer* in the same lake nests later than the other species of turtles, as a rule not earlier than the middle of June (but as early as June 10, *op. cit.*:132), and rarely later than the middle of July; he observed deposition of eggs on June 22. Sites of deposition of eggs were mostly in soft sand not more than six feet from water; other sites found by Newman (*op. cit.*:132-33) were a sandy, abandoned road bed separated from the shore by a strip of tall grass, a rock pile (the eggs being dropped into crevices and sand packed around them), among roots of a tree (the eggs being deposited between the roots and under them in a very irregular fashion), and in clay "so hard packed that one could scarcely break it with the fingers." Natural nest sites in hard clay and a rock pile seem incongruous with nesting habits of softshells. I note that Newman's study was not begun until 1902 (*op. cit.*:127), and it was that year that the water level of the lake was high, flooding the surrounding lowlands (Evermann and Clark, 1920:49-53). Perhaps some of the nests found by Newman were old and not natural because of conditions resulting from the receding water level.

Newman (*op. cit.*:134-35) mentioned that in small sandy areas nests were frequently in contact and overlapped; he found one nest containing nine small eggs contiguous with 23 large eggs. Breckenridge (1944:187) reported a nest of 56 eggs of two slightly differing sizes, and probably from two females. Evermann and Clark (1920:594) discovered "probably 10 or 12 nests in a distance of a few yards" and mentioned one nest containing 25 eggs "that evidently belonged to two different sets . . . In the bottom were 10 eggs that looked old . . . and . . . separated from them by sand, were 15 other eggs."

Nesting sites of *muticus* were mentioned by Muller (1921:181) on one of several small islands having "gently sloping sand and mud shores, and interior areas of open sand and densely growing willows" in the Mississippi River, near Fairport, Iowa. The same author wrote that the egg-laying season is from late June to early July, and that the female selected a place 10 to 60 feet inland "with an unobstructed view of the open water." Farther north on the Mississippi River near Dubuque, Iowa, Goldsmith (1945:447) found that *muticus* preferred "clean, somewhat level sandbars and sandy shores free from trash, weeds . . . and exposed to open view." The same species, however, may "make unsatisfactory nests . . . in any place they can find sand, even in the weeds and bushes . . . when the river is high, covering the sandy plots . . ." Sometimes nests, which were "seldom nearer than six feet or more than twenty-five feet from water . . .," were submerged by a rise in water level. In Missouri, Hurter (1911:251) found that individuals of *muticus* came ". . . out on the sandbars in the Mississippi River to deposit their eggs . . . At the end of May up to the middle of June . . ." Cahn (1937:182) wrote that the nesting season of *muticus* is early July near Meredosia, Illinois. Anderson (1958:212, Fig. 1) found nests of *muticus* along the Pearl River in Louisiana on an open sandbar (not in gravel, fine sand or silt), whereas nests of *Graptemys* were confined to the landward margin of the sandbar.

The onset and length of the breeding season seems to be geared to the climatic conditions under which the species occurs, and, as would be expected, begins earlier and lasts longer in southern latitudes than in northern latitudes. The period of deposition of eggs in *T. ferox* (Florida) is from late March to mid-July, whereas that of northern populations of *spinifer* and *muticus* (southern Great Lakes region) is usually from mid-June to mid-July.

Seemingly there is little difference between species in preference of nesting sites; a sandy substrate is probably preferred. Gravid females of *ferox* and *spinifer* may wander overland some distance and select places where the view of the water is obstructed by vegetation; both species may wander little and nest in full view of the water. Concerning *muticus*, it is of interest that of the many nests discovered by Anderson (*loc. cit.*) on an open sandbar, all were those of *muticus* and none was a nest of *spinifer*. The nests of *muticus* mentioned by Muller (*loc. cit.*) and Goldsmith (*loc. cit.*) were on open sandbars. On June 4, 1953, six clutches of eggs were found on an open sandbar of the Escambia River, Florida; all hatchlings from those eggs that were successfully incubated were *muticus*. On June 1, 1954, three nests were found on an open sandbar of the same river (Pl. 50); the temperature within the nests at 6:30 a. m. was approximately 25° C. Two nests were dug in a sand substrate on the level portion of the bar (Pl. 51, Fig. 1). The third clutch of eggs was deposited in a sand-gravel substrate at the brim of the incline from the shore (approximately 30 degrees and about five feet above the water); the eggs of this clutch were arranged rather symmetrically (Pl. 52, Fig. 2). Unfortunately, most of the eggs from these three clutches failed to hatch. Although the data are far from conclusive, I have the impression that *muticus* limits its sites of egg deposition to the open regions of sand bars and does not lay inland where it must traverse vegetated areas unless preferred nesting sites are submerged or otherwise unsatisfactory. Females of *spinifer* may utilize open sandbars for deposition of eggs but not areas where *muticus* occurs. In areas where both *muticus* and *spinifer* occur, the latter probably lays farther inland or on the landward margins of sandbars.

Excavation of nests has been observed in *ferox* (Hamilton, 1947:209), *muticus* (Muller, 1921:181-82; Goldsmith, 1945:448), and *spinifer* (Newman, 1906:132-33; Cahn, 1937:191-92; Breckenridge, 1960:284). Turtles leaving the water are cautious, usually stopping and extending the neck to its greatest length, holding the head high, and sometimes returning to the water for a short time. Depending on the condition of the substrate and wariness of the female, nest construction may begin immediately, or several holes may be dug and then abandoned. The excavation on level ground or a slight incline is made by means of the hind feet (Muller mentions digging with the forefeet; I agree with Pope, 1949:321, and Conant, 1951:264, who consider Muller in error); the forefeet are firmly planted and not moved during the excavation, deposition of eggs or the filling of the nest cavity. The hind feet are used alternately; cloacal water may be used to facilitate digging or to provide a suitable substrate for the eggs. Cahn mentioned that some sand may be flung four or five feet, and that during the digging the head is held high. Breckenridge (*loc. cit.*) reported that sand was thrown a distance of ten feet. The nest may be completed in 16 minutes (Cahn, *loc. cit.*) or less than 40 minutes (Newman, *loc. cit.*). Breckenridge recorded 17 eggs laid in six minutes, Cahn recorded 12 eggs laid in eight minutes, and Hamilton recorded four eggs laid in three minutes. The hind feet are used to arrange the eggs and are used alternately to fill the nest cavity; sometimes a little sand is scraped in before all the eggs are deposited. Muller recorded the nest cavity as five inches in diameter and ten inches deep, the finished nest appearing "as a small crater . . . about a foot in diameter, or where the surface is covered with pebbles, as a circular area of clear sand." Goldsmith reported that the nest cavity was six to nine inches in depth, and that after deposition and filling with sand "By certain twisting movements with all four legs, she drags the plastron around over the sand, making a perfect camouflage." Newman found the nest flask-shaped having a depth of about six inches, and diameters of about three inches at the bottom and one and one-half inches in the neck. Hamilton described a flask-shaped nest, the entrance of which would "barely permit the passage of an egg . . . the bottom, at a depth of five inches, being about the width of a quart milk bottle." Cahn related that the "hole descended at an angle of about 60°," and the eggs thus rolled down an inclined plane.

Possibly the nests of *ferox* and *spinifer* differ from those of *muticus* in being flask-shaped. A nest of *spinifer* was reported by Gehlbach and Collette (*loc. cit.*) as having a neck three inches across, a depth of six inches and a width of five inches at the bottom. The nests of *muticus* that I discovered on the Escambia River were not flask-shaped; the eggs were five to seven inches below the surface. Evermann and Clark (1920:594) reported eggs of *spinifer* "generally at a depth of four to ten inches," and Breckenridge (*loc. cit.*) found the topmost eggs about five inches below the surface. There may be behavioral differences between *ferox* and *spinifer* and *muticus*. Hamilton (*loc. cit.*) mentioned that *ferox* proceeded with its reproductive duties even when he stood only a few yards away. Muller (*op. cit.*:181) found that *muticus* would run to the water if disturbed, without completing deposition of eggs; the same behavior was described by Cahn (*op. cit.*:191) for *spinifer*. Newman (1906:133) wrote that *spinifer* will abandon nesting activities if surprised before egg deposition begins, but will wait to cover the eggs if interrupted while laying eggs. Goldsmith (1945:448) found that an observer did not disturb females of *muticus* when they were laying eggs (females "could be approached and even touched"), but that, in the presence of an observer, they would scurry toward the water without covering the eggs and would not return to cover them. Turtles frightened in the process of the construction of the nests would not return to complete the original nest. Harper (1926:415) wrote that *ferox*, after completing nesting activities, will crawl a few feet from the nest and scuffle up the surface, presumably to decoy predators that might otherwise destroy the eggs; this observation has not been corroborated by other authors. Harper (*op. cit.*:416) recorded the observation of Allen Chesser, who says that females, after egg deposition, often ". . . bury themselves, before they go ter the water, an' stay there ten er twelve hours."

Reproductive Potential

Estimates of reproductive potentials are subject to variation of one kind or another. Counts of oviducal eggs or those in nests may be misleading, as in some individuals one or more eggs may have been deposited previously. Mitsukuri (1905:263), Newman (1906:135), Muller (1921:182), and Cahn (1937:183) have mentioned that the number of eggs per clutch corresponds to the size of the female. Females of northern populations may have larger clutches than females of the same size from southern populations.

TABLE 8. RECORDS IN THE LITERATURE PERTAINING TO NUMBER AND SIZE OF EGGS OF THREE AMERICAN SPECIES OF TRIONYX.

SPECIES	Number of eggs per clutch; oviducal (o), nest (n); ave. = average	Size of eggs; ave. = average	Authority and remarks
ferox.....	....	24 mm.	Agassiz (1857, pl. 7, fig. 20); nat. size.
	22 (n)	ave. 31 mm.	Wright and Funkhouser (1915:120)
	some (o)	32 mm.	"
	20 (o)	ave. 25 mm., and 12 gms.	Goff and Goff (1935: 156)
	17 (o)	ave. 27 mm.	Hamilton (1947:209)
	21 (o)	....	"
	7 (o)	....	" (egg deposition probably interrupted)
spinifer...	....	29 mm., 26.5 mm.	Agassiz (1857, pl. 7, figs. 20 and 23, respectively); nat. size.
	9, 12, 17, 18, 27 and 32	....	Eigenmann (1896: 263); northern Indiana
	9 to 24, ave. 18	....	Newman (1906:135); northern Indiana
	about 30 (n), 4 (n), 3 (n)	1.09 x 1 inch	Evermann and Clark (1920:593-94); northern Indiana
	21 (n and o)	(o) and some (n) .93 x .93 inches; rest of (n) 1.07 x 1.07 inches	"
	32 (o)	ave. 1 1/4 inches	Force (1930:38); Oklahoma
	9, 12, 13, 15, 17, 19, 19, 21, 22, 23, and 25; ave. 18	ave. 28.3 mm. (217 eggs)	Cahn (1937:193); Illinois
	12 (o), 26 (o), 24 (n), and 30 (n)	22.0 to 28.5 mm.	Breckenridge (1944: 187); Minnesota

TABLE 8. RECORDS IN THE LITERATURE PERTAINING TO NUMBER AND SIZE OF EGGS OF THREE AMERICAN SPECIES OF TRIONYX.—*Concluded.*

SPECIES	Number of eggs per clutch; oviducal (o), nest (n); ave. = average	Size of eggs; ave. = average	Authority and remarks
spinifer (*concluded*)	21 (o)	24 to 27.8 (ave. 25.6 mm.) x 25.8 to 29 (ave. 27 mm.)	Conant (1951:160); Michigan
	22 (n), 22 or 23 (n)	....	Hedrick and Holmes (1956:126); Minnesota
	25 (n)	ave. 24 x 25.2 mm.	Gehlbach and Collette (1959:142); Nebraska
	17 (n)	....	Breckenridge (1960: 284); Minnesota
muticus...	....	about 22 mm.	Agassiz (1857, pl. 7, fig. 21); nat. size.
	21	about 20 mm.	Hurter (1911:249); Missouri
	4, 12, 13, 16, 21, 22, 26, and 33, all (n); ave. 22	ave. 2.3 cm. and 7 gms.	Muller (1921:182); Iowa
	18 to 22, maximum 31	ave. 22.6 mm. (116 eggs)	Cahn (1937:183); Illinois
	93 from 5 nests, ave. 18.6; 10, 10, 16, 17, 17, 19, 21, 21, 22, 22, 31, all (n), ave. 18.7	variable—largest *ca.* 1 3/8 inches, smallest less than one inch.	Goldsmith (1945: 449); Iowa

Published statements pertinent to an assay of the reproductive potentials of each species are limited to counts of eggs found in oviducts or nests (Table 8). Counts of eggs made by some authors obviously include enlarged ovarian follicles, which were not distinguished from the eggs in the oviducts. True (1893:152) stated that "The number of eggs is large, varying from thirty or forty to sixty or seventy." Surface (1908:123) mentioned that the "eggs may reach about sixty in number," and Lesueur (1827:262) mentioned 50 to 60. Wright and Funkhouser (1915:120) wrote that a female "contained 49 embryonic eggs" and (*op. cit.*:122) mentioned embryonic eggs ranging in size from 15 to 32 millimeters in diameter and bright orange or white. Hamilton (1947:209) recorded more than 50 ovarian eggs approximating a marble in size.

Additional records of size of clutch are provided by data from dissected females (Table 9). All females were collected from May through September from localities south of latitude 36.5°. The number of eggs includes those in both oviducts, and the number of ovarian follicles those in both ovaries. The number and range in size of only the largest group of follicles is listed; in some instances the size of follicles formed a graded series, and the designation of a group was arbitrary.

Published data (Table 8) indicate that the average number of eggs per clutch for the three American species is about 20, although the number of eggs may exceed 30 in *spinifer* and *muticus.* Except for those of *ferox,* most of these records are based on observations in northern latitudes (approximately 40°). My examination of females from southern latitudes (below 36.5°) reveals no oviducal egg count greater than 17 and an average number of eggs per clutch of 9.6 per *spinifer* (Table 9); that of *muticus* is 7.3, as based on data given in Table 9 as well as on egg-nest counts of 15, 6, 6, 6, 6,

TABLE 9. LENGTH, NUMBER OF OVIDUCAL EGGS, AND CONDITION OF OVARIES IN ADULT FEMALES OF T. SPINIFER AND T. MUTICUS.

SPECIES	Size of female (plastral length, cm.)	Eggs (total)	Ovarian follicles (total)	
			Number	Size (mm.)
muticus...........	14.4	6	14	15–18
	16.3	9	4	15–17
	16.5	....	3	16
	16.5	3	4	14–18
	17.2	....	13	14–21
	27.0	....	25	18–21
spinifer...........	16.2	7	4	16–20
	16.2	7	5	18–20
	16.2	7	1	18
	16.3	6	5	16–18
	16.3	4	5	15–19
	16.8	6	1	18
	17.3	3	2	17
	18.3	....	13	19–20
	19.5	....	2	17
	19.8	....	4	20
	20.7	....	11	15–18
	21.5	....	6	8–11
	22.0	....	13	11–14
	23.5	8	12	20–24
	25.5	11	several	18–22
	25.8	13	?	18–21
	26.8	10	5	18–20
	30.5	13	5	20–21
		16	16	16–21
		11	19	15–20
		17	23	18–22
		17	22	14–20
		8	15	18–22

5, 9, 8, and 8. Ovarian follicles larger than 15 millimeters in diameter are arbitrarily considered to comprise the next clutch that will be deposited in the current season. Follicles of this size possibly are retained until the following year or some may undergo regression; some of the included follicles may not be representative of the succeeding egg complement. The average number of follicles of the most enlarged groups is 9.0 for *spinifer* and 10.5 for *muticus*. Females in northern latitudes probably have a greater reproductive potential than those in southern latitudes if it is assumed that there is only one laying per season for an individual; the maximum number of eggs laid at any one time probably does not exceed 35. There is also an indication that larger females deposit more eggs than smaller females (Table 9). Muller (1921:184) mentioned two double eggs (each having two yolks) in the complement of 33, indicating an abnormally large number and excessive crowding of eggs in the oviducts. Simkins (1925:188) also mentioned some eggs of a clutch (form and locality unknown) that were five or six millimeters larger (about 31-32 mm.) than the rest, and which "invariably bore twins." The largest number of eggs in a single nest mentioned by Simkins is 22. If the presence of double-yolked eggs is indicative of crowding of eggs in the oviducts, the egg complements of 22 and 33 indicate the approximate maximal number of eggs per clutch. In the species *spinifer*, the average size of sexually mature females is slightly smaller at some places in the south than in the north. Therefore, smaller clutches are to be expected in the south.

Many of the females collected in June or July contained corpora lutea four to eight millimeters in diameter in addition to enlarged ovarian follicles. Presumably the corpora lutea indicate clutches deposited earlier in the current season, and the enlarged follicles represent clutches to be deposited in the current season. One female of *muticus* (OU 27593) obtained on July 10, contains oviducal eggs, ovarian follicles 15-17 millimeters in diameter, and corpora lutea of different sizes that exceed the number of oviducal eggs; possibly this female was capable of laying three clutches each season. Corpora lutea, representing ovulation points of eggs in the oviducts, are approximately eight millimeters in diameter. In order to establish definitely the reproductive potentials of any species of turtle, it is desirable to know the approximate size of ovarian follicles that are retained by sexually inactive females, and the rate of regression of the corpora lutea. The data suggest that, in southern populations at least, two and possibly three clutches of eggs are deposited in the annual breeding season. Mitsukuri (*in* Cagle, 1950:38) found that *T. sinensis* deposited four groups of eggs each season.

It is suggested that the seasonal reproductive potential of northern populations (averaging about 20 eggs per clutch, and probably one clutch per season) is less than that for southern populations (averaging about 10 eggs per clutch, but three clutches per season). But owing to variation, there may be no great discrepancy between the actual potentials of northern and southern populations.

Eggs

The eggs of *Trionyx* are white and spherical having a brittle shell. Some eggs are occasionally abnormal in shape and size; overcrowding of eggs in the oviducts may result in small, irregular-shaped eggs, or large double-yolked eggs. Presumably enlargement of the eggs occurs in the oviducts and within a short period after deposition prior to complete hardening of the brittle shell; therefore some eggs in the oviducts are smaller than those in nests.

The data concerning *ferox* (Table 8) suggest that the maximum size of eggs is 31 to 32 millimeters, whereas oviducal eggs are slightly smaller, about 25 to 27 millimeters. Eggs of *spinifer* from northern latitudes (most from approximately 40°, Table 8) also vary in size, oviducal eggs being as small as 22 millimeters in diameter and the maximal size about 29 millimeters. Average extreme measurements (in mm.) of oviducal eggs (number of eggs in parentheses) from females taken in latitudes of 33 degrees or less are: 25 x 29 (11), 29 x 30 (11), 28 x 30 (13), 28 x 30 (10), 29 x 30 (5), 29 x 29 (8), 25 x 26 (17), 29 x 30 (5), and 28 x 29 (8). The average size of these eggs is slightly larger than the oviducal eggs of which measurements are given in Table 8, and suggest larger eggs from more southern latitudes. Eggs of *muticus* are smaller than those of *spinifer* (Cahn, 1937:183) or *ferox;* the average size of eggs from nests found in Iowa and Illinois is 22 to 23 millimeters (Table 8). Nine oviducal eggs from a female obtained in Lake Texoma, Oklahoma, averaged 22 x 23 millimeters. The largest eggs of *muticus* are from the southernmost locality; eight eggs from a nest found along the Escambia River, Florida, averaged 26 x 27 millimeters.

In general, the data suggest that at each laying slightly smaller eggs but larger numbers are laid by females in northern latitudes, whereas larger but fewer eggs are laid by females from farther south.

Incubation and Hatching

Length of the incubation period seems to depend upon conditions of heat and moisture, and, in general, to be geared to the prevailing climatic conditions. Goff and Goff (1935:156) artificially incubated some eggs of *ferox* at temperatures varying from 82.3 to 89.2° F., and found that the incubation period was 64 days. Muller (1921:184) wrote that the period of incubation of eggs of *muticus* (natural nests at temperatures about 90°., *op cit.*:182, and artificial nests) in Iowa is from 70 to 75 days. Breckenridge (1944:187) stated that *spinifer* makes nests in Minnesota from June 14 to July 6, and cited reports that indicate hatching in September. Hedrick and Holmes (1956:126) discovered a nest of eggs in Minnesota on September 5; the eggs were artificially incubated and some hatched on October 29. Eigenmann (1896:263) found eggs as late as September in northern Indiana that "contained young which would have been ready to hatch about a month later." Cahn (1937:193) wrote that *spinifer* in Illinois lays in June or early July and that "young-of-the-year are taken in late August and September." Some recently deposited eggs of *muticus* (as indicated by fresh turtle tracks, Pl. 50, Fig. 2) that I obtained on June 1 were artificially incubated and hatched on August 4, indicating an approximate incubation period of 65 days. Dr. Paul K. Anderson in the course of field work on the Pearl River, Louisiana (1958:211), found that eggs collected on June 13 from a nest excavated three to five days before, hatched on August 15, indicating an incubation period of approximately 67 days. Eggs collected on May 17 to 25 (three clutches) hatched on August 4 to 6, indicating an incubation period of approximately 77 days. In any latitude the incubation period probably is at least 60 days. Eigenmann (*loc. cit.*), however, mentioned empty nests that were found in July; this indicates early hatching or more probably the action of predators.

In northern latitudes eggs or young turtles may over-winter in the nest if deposition is late in the season. In northern Indiana Evermann and Clark (1920:595) found a nest on November 16 that contained "well-formed young" and believed that the turtles would have wintered in the nest. Conant (1951:160) was of the opinion that most eggs probably hatch in early fall, but that some do not hatch until spring.

The hatching of eggs of *muticus* has been described by Muller (1921:183). According to him, the forelimbs first emerge through the shell and enlarge the opening. There is an "egg tooth below the flexible proboscis" but "it does not seem to be used in escape from the eggs, and is dropped a week after hatching." Hatchlings burrow almost straight upward through the sand leaving the egg shell below the surface and a hole in the sand about an inch in diameter. Muller found that young turtles emerge from the nests in the night or early morning and always go downhill probably influenced in their movements by the open sky and sloping beach. Anderson (1958:212-15) found that hatchlings of *muticus* leave nests within the first three hours after sunset and travel a direct route to the water. He discovered that hatchlings are active on the surface of the sand at night and generally show a positive reaction to light (moonlight, flashlight), whereas, in daytime, there is a negative reaction to bright sunlight (causing the turtles to bury themselves in sand). Anderson believed that the positive response to light at night is not correlated with the water-approach behavior of hatchlings, but that movements to water are possibly influenced by a negative reaction to dark masses of environment (such as shadows formed by landward forests).

Age and Growth

Goff and Goff (1935:156) found that hatchlings of *ferox* average 8.82 grams (extremes, 8.50 to 9.25); one of these, UMMZ 76755, is illustrated in Plate 31. Muller (1921:184) recorded measurements of five hatchlings of *muticus;* the average measurements (in cm., extremes in parentheses) were: length of carapace, 3.54 (3.43 to 3.67); width of carapace, 3.20 (3.10 to 3.25); length of plastron, 2.54 (2.47 to 2.60). I recorded measurements of 32 hatchlings (three clutches combined) of *muticus* on August 16; the turtles hatched on August 4 to 6 from eggs collected along the Pearl River, Louisiana. The average measurements (in mm., extremes in parentheses) of the 32 turtles were: length of carapace, 41.3 (34.0 to 45.0); width of carapace, 38.6 (31.0 to 40.0); length of plastron, 30.1 (25.0 to 32.0). These turtles have circular umbilical scars averaging approximately two millimeters in diameter. The smallest hatchling that I have seen measures 21.0 millimeters in plastral length (*T. m. muticus,* INHS 3458). There are no data to indicate a difference in size of hatchlings among the American species of soft-shelled turtles. The average plastral length of most hatchlings probably is 28.0 to 30.0 millimeters.

Owing to the lack of a horny epidermal covering of the carapace and plastron, soft-shelled turtles are not so well suited to studies of age and growth as are the "hard-shelled" species, which have visible impressions of growth annuli on the epidermal scutes. Mattox (1936:255) found annular rings in the long bones of specimens of *Chrysemys* and suggested that it is tenable to correlate the number of rings with the age of the turtle.

Mitsukuri (1905:265) reported that in hatchlings of *Trionyx sinensis* the length of the carapace averages 2.7 centimeters (hatchlings of *sinensis* seem to average smaller than any American species), and that the average length of carapace (cm.) at the end of the first year is 4.5, second year 10.5, third year 12.5, fourth year 16.0, and end of fifth year 17.5; he stated also that females of *sinensis* are sexually mature in their sixth year. Breckenridge (1955:7-9) computed a growth curve based on 11 recaptures of females of *spinifer* in Minnesota; his data on rate of growth for the first five years do not differ appreciably from those of Mitsukuri. As most females of *spinifer* are sexually mature when the carapace is about 11 inches long, the age at sexual maturity is approximately 12 years according to Breckenridge (*op. cit.*:8, Fig. 4). The discrepancy in age of females at the size of attainment of sexual maturity (Mitsukuri—six years; Breckenridge—12 years) is, in part, rectified by the fact that *Trionyx sinensis* probably is a smaller species. Also, Breckenridge's computation of the growth curve is based on continuously decreasing increments of growth and seemingly eliminates consideration of the probable marked decrease in rate of growth that occurs when sexual maturity is attained—a phenomenon noted in other species of turtles. I think that increments of growth of immature turtles are, on the average, larger than those of sexually mature turtles. Judging from these criteria, the age of a female of *spinifer* at sexual maturity is less than 12 years, and turtles having carapaces 17 to 18 inches in length (maximal size for *spinifer*) would be older than 53 years (*op. cit.*:9). Occasional individuals, however, may greatly exceed the usual growth rate in which event large adults may be younger than 50 years.

Females of *muticus* are sexually mature when the plastron is 14.0 to 16.0 centimeters long, which corresponds to a carapace 19.6 to 22.4 centimeters (about 7¾ to 8¾ inches) long (average CL/PL approximately 1.4, see Fig. 13). The smaller adult females probably mature sexually in their sixth year, but most probably do so when seven years old. Accordingly, some *T. spinifer emoryi*, which are sexually mature at a plastral length of 16.0 centimeters, are also sexually mature in their seventh year, whereas most *spinifer* (sexually mature at a plastral length of 18.0 to 20.0 cm., corresponding to a length of carapace of 25.2 to 28.0 cm. or about 10 to 11 inches) probably become sexually mature in their ninth year, and some when eight years old. Most males of *spinifer* are sexually mature when the plastron is 9.0 to 10.0 centimeters long (length of carapace 12.6 to 14.0 cm. or 5 to 5½ inches), whereas males of *muticus* and some *T. spinifer emoryi* are sexually mature at a plastral length of 8.0 to 9.0 centimeters (length of carapace 11.2 to 12.6 cm. or 4½ to 5 inches). The smaller adult males are probably sexually mature in their fourth growing season. Breckenridge (*op. cit.*:7, Tab. II) commented on the abundance of females between five and 12 inches in length, and males that ranged in length from five to seven inches. The abundance of turtles in these size ranges is probably due, in part, to a slowing of the rate of growth indicating the approach of sexual maturity; the abundance of the smallest males is especially in accord with the size at sexual maturity of males (about five inches).

The largest acceptable record of size of *spinifer* is 18 inches in length of carapace (Breckenridge, 1957:232). Stockwell (1878:402), however, wrote that females of *spinifer* attain "an extreme length of from twenty-four to twenty-eight, and, in rare instances, thirty inches, with an average length of carapace of fifteen to eighteen," and True (1893:152) mentioned lengths of two feet or even more. Turtles 17 to 18 inches long are doubtless rare and probably about 60 years old. A specimen of *ferox* lived the longest time in captivity—25 years (Pope, 1949:304). Individuals of *ferox* probably exceed the maximum recorded length of carapace of 18½ inches (Agassiz, 1857:401). The head of a *ferox* having a width of 3½ inches (Wright and Funkhouser, 1915: 120) corresponds to a length of carapace of approximately 22½ inches (PL/HW = 4.9; CL/PL = 1.3). De Sola and Abrams (1933:12) wrote that *ferox* in the Okefinokee Swamp, Georgia, attains a length of two feet. The largest female of *muticus* of which I have record is 21.5 centimeters in plastral length (KU 2308), a measurement corresponding to a carapace about 13 inches long.

Mortality

Man, in one sense or another, is a great enemy of soft-shelled turtles. Those caught by fishermen are destroyed because of the erroneous belief that they are harmful to fish populations. Some are drowned in hoop-nets or gill nets used by commercial fishermen. Many softshells are used by man for food. Herald (1949:118-19) reported the results of spraying an area with DDT and mentioned a 10-inch individual of *ferox* that was eating a dead bluegill, and which "probably died as a result of ingesting contaminated food."

Predation on eggs probably accounts for most mortality. Hamilton (1947: 209) reported tracks of spotted skunks, raccoons and foxes seen about destroyed nests, and Cahn (1937:183) incriminated skunks and raccoons. Goldsmith (1945:449) reported a raccoon that unearthed seven nests in one night. Little and Keller (1937:221) wrote of egg shells found in the sand (probably not as a result of hatching), and Muller (1921:182) reported egg shells around dug-up nests, suggesting such predators as "ground moles," raccoons and crows. Chesser (in Harper, 1926:416) said that in the Okefinokee Swamp the jackdaw (fish crow), raccoon, bear and domestic dogs will eat the eggs. Wright and Funkhouser (1915:122) recorded a young *ferox* in the stomach of a water moccasin (*Agkistrodon piscivorous*), and suggested that young softshells probably are food of larger snakes. Kellogg (1929:26) wrote that stomachs of two alligators each contained one soft-shelled turtle. Newman (1906: 136) found that young captives were eaten by individuals of *Chrysemys* and *Sternothaerus*, and I found that they were eaten by *Kinosternon*. Mitsukuri (1905:261-62) stated that first- and second-year individuals of *T. sinensis* are eaten by the adults.

Breckenridge (1960) wrote that a clutch of eggs probably failed to develop because of an ". . . unusually cool season." Evermann and Clark (1920:595) stated that "many young appear to perish during the first winter." They (*op. cit.*:594) found two eggs submerged in two feet of water and it is supposed that they never hatched. Dundee (1950:139) reported remains of soft-shelled turtles left on the mud of a dried swamp.

Parasites

Muller (1921:182) found maggots in a few eggs of a clutch, but thought that only the infertile and decomposing eggs were infested. I removed a hard, spherical cyst from the hind leg of a preserved softshell (TU). A captive hatchling (TU 17304) died as the result of a continuously enlarging and deepening hole on the top of its head; I could not discern a visible parasite with the naked eye. I found 25 leeches (*Placobdella parasitica*, largest about 13 mm.; identified by Dr. Kenneth B. Armitage, Department of Zoology, University of Kansas) in association with 11 *T. m. muticus* (number per turtle not known) that were collected from the Kansas River at Lawrence, Douglas County, Kansas. Evermann and Clark (1920:596) reported a few nematodes in the stomachs of some *spinifer,* and three nematodes are listed by Harwood (1932:46, 60, 62, 66) in the same species. Hughes, Higginbotham and Clary (1941) have listed the known reptilian hosts of parasitic trematodes, and Hughes, Baker and Dawson (1941) have done the same for tapeworms. The species of parasites and their trionychid hosts are listed below.

	TREMATODA	
Trionyx ferox:	*Neopolystoma orbiculare*	*Vasotrema amydae*
	Neopolystoma rugosa	*Vasotrema attenuatum*
	Polystomoides coronatus	*Vasotrema robustum*
	Teloporia aspidonectes	
Trionyx muticus:	*Crepidostomum cooperi*	*Opisthorchis ovalis*
Trionyx spinifer:	*Hapalorhynchus evaginatus*	*Vasotrema amydae*
	Opisthorchis ovalis	*Vasotrema attenuatum*
	Polystomoides coronatus	*Vasotrema longitestis*
	Teloporia aspidonectes	*Vasotrema robustum*
	CESTODA	
Trionyx ferox:	*Proteocephalus trionychinus*	
Trionyx spinifer:	*Proteocephalus testudo*	
	NEMATODA	
Trionyx spinifer:	*Camallanus trispinosus*	*Spiroxys amydae*
	Falcaustra chelydrae	

Economic Importance

Several authors have mentioned softshells as a food item much sought after by man. The commercial value of these turtles has been summarized by Clark and Southall (1920:15-16). Softshells are consumed in quantity only in small towns near the place of capture. They are found only occasionally in the markets of large cities because the turtles are little known and the palatability of their flesh is unappreciated. Also, they do not stand shipment so well as other turtles, and they are "not so meaty as the snapper; so there is more waste" (Clark and Southall, *loc. cit.*). Little and Keller (1937: 221) reported living individuals for sale at the market in Ciudad Juarez, Chihuahua; however my inquiry at markets in Juarez in the summer of 1959 disclosed no evidence of recent sale of soft-shelled turtles. In the southeastern United States the demand is perhaps greater than in other regions. I have noted softshells in the market at New Orleans, and Oliver (1955:19) has mentioned the sale of "some 146,600 pounds" in one recent year in Florida. Over most of their range, however, there probably is no general demand for softshells and no special efforts are made to capture them. Softshells have been raised successfully on "turtle farms" in Japan (Mitsukuri, 1905). True (1893:152) wrote that "The eggs also are considered very excellent."

Softshells generally are condemned by fishermen because of the mistaken belief that they are detrimental to fish populations. Food of softshells is principally crawfish and insects. Fish comprise a small proportion of the diet (frequency 1.9% in Michigan, Lagler, 1943: Tab. 9). Most of the fishes eaten seem to be small minnows. Probably fish would comprise a larger percentage of the diet if they could be caught. I doubt that a softshell can pursue and capture a healthy fish in natural waters. Recently dead fish are eaten and perhaps fish eggs, and senile and decrepit fishes. There is no evidence that soft-shelled turtles are active predators on any kind of fish. Of course in congested areas such as ponds of fish hatcheries, it is desirable to eliminate the turtles. The known food habits of soft-shelled turtles suggest that they compete with game fishes for food, but there is no information on the intensity of competition (Lagler, *op. cit.*:305).

The combined statements of many authors in their general accounts of food habits (for instance, Babcock, 1919:425) have tended to create the erroneous belief that soft-shelled turtles harm waterfowl. To my knowledge the only basis for this belief is the statement of Wright and Funkhouser (1915:123) that according to the natives of the Okefinokee Swamp, the larger turtles "devour also such waterfowl as are unfortunate enough to be taken unaware by these reptiles." Perhaps an occasional waterfowl is eaten, but the present information on kinds of food eaten certainly does not warrant the destruction of soft-shelled turtles. There may be some mortality in congested areas such as game refuges where young birds crowd the surface of the water.

The kind of bait successfully used in trapping softshell turtles suggests that they are of some value as scavengers.

EVOLUTIONARY HISTORY

Before attempting to reconstruct the history of soft-shelled turtles in North America, it will be helpful to summarize the salient facts concerning the distribution and relationships of the living forms, and to comment on fossils.

Distribution

The geographic range of the family Trionychidae in North America is principally in the eastern two-thirds of the continent and contributes to the well-known floral and faunal resemblance of eastern North America to that of eastern Asia (Schmidt, 1946:149) because *Trionyx ferox* (see Fig. 18) resembles the species of the genus in Asia more closely than it does any North American species. The Recent distribution in America does not include the Neotropical region, whereas the geographical range in the Old World extends south of the equator (Fig. 1; Dunn, 1931:109, fig. 2; Gadow, 1909:333, fig. 72; Hay, 1908:35, fig. 16).

American softshells occur in all river systems in the United States and the two adjacent river systems on the east coast of México that drain into the Gulf of México. Softshells inhabit streams of the Great Plains and occur westward to the foothills of the Rocky Mountains in the western tributaries of the

Mississippi River. Only *T. s. spinifer* occurs in the southern part of the Great Lakes-St. Lawrence drainage. Softshells are absent from the Atlantic Coast drainage except the Hudson River and those rivers at least south of (and including) the Pee Dee River in South Carolina.

T. s. emoryi is not known to be indigenous west of the Río Grande drainage, and has probably been introduced across the Continental Divide via the Gila River in western New Mexico into the Colorado River drainage of Arizona (Miller, 1946:46); the species undoubtedly occurs in México on the Sonoran side of the Colorado River opposite Baja California (Bogert and Oliver, 1945: 417).

In the summer of 1959, I trapped turtles and with a specimen in hand inquired about softshells occurring in the inland drainages of northern México. From two collecting stations on the Río Nazas in Durango, only specimens of *Pseudemys* and *Kinosternon* were obtained; local inhabitants had neither seen nor heard of softshells. Flooded conditions in August of 1959 permitted trapping in only one of the inland drainages of northwestern Chihuahua, the Río Santa María; only specimens of *Kinosternon* were obtained. Local residents near that river as well as those living near the Río Casa Grandes and Río del Carmen had not seen or heard of softshells. A person that I judge to be a competent observer reported seeing a softshell in June of 1958 in the Río Alamos (Arroyo Cuchujáqui) near Alamos, Sonora, in the Río del Fuerte drainage on the west coast of México. I was a member of a field party from the University of Kansas that visited that locality in late January of 1959; only specimens of *Pseudemys* and *Kinosternon* were collected. Possibly isolated populations occur in streams of the Pacific Coast drainage of northern México. If so, they may have entered Pacific Coast drainages by stream capture across the Continental Divide. Several species of fish that are characteristic of the Río Grande traversed the Sierra Madre Occidental at some former time (presumably via the Río Conchos and Río Papigochic) and occur in the Yáqui River drainage (Meek, 1904:xxxviii, xlvii; Miller, 1959:214-15, 217). Because of the probability that the Río Nazas at some former time flowed north into the Río Grande (Meek, *op cit.*:xxxiv), it is notable that softshells are absent in the Río Nazas drainage; the Big Bend turtle, *Pseudemys scripta gaigeae,* occurs in both drainages.

Relationships

Characters of *Trionyx ferox* suggesting a closer resemblance to some Old World members of the family than to the other three American species are: large size; marked difference between juvenal and adult patterns on the carapace; the marginal ridge; and the longitudinal ridgelike prominences on the carapace, especially in juveniles. Other characters of *ferox* suggesting a corresponding, but less marked resemblance to Old World species of *Trionyx* are: the large size of the eighth pair of pleurals; the absence of callosities on the epiplastron and preplastra; frequent fusion of the hyoplastra and hypoplastra (more than in *spinifer* or *muticus*); and tolerance of marine waters (more than *muticus* or *spinifer*). Some fossils also suggest alliance with *ferox* and some Old World members of the genus in their large size, large eighth pair of pleurals, and occurrence in marine deposits; several Old World species have been reported at sea (*Pelochelys, T. triunguis, T. sinensis*). *T. ferox* is monotypic and has the most southeasterly displaced, geographic range.

Because *ferox* resembles softshells from the Old World more closely than it does any American species, *ferox* is assumed to be more closely related to Old World softshells than to any American species, and, because of resemblance to some fossils, *ferox* is assumed to resemble most closely the primitive, ancestral stock of softshells that occupied North America. *T. spinifer, T. muticus* and *T. ater,* which resemble each other more closely than any of them resembles *T. ferox* or any Old World species, are considered autochthonous in North America. *T. spinifer* and *T. muticus* are distinct, sympatric species. Burt (1935:321) suggested that the two species "may be variants of the same species." *T. ater* is weakly differentiated from *T. spinifer emoryi.* The species, *ferox, spinifer* and *muticus* are well-differentiated and were considered by Agassiz (1857), Gray (1869) and Baur (1893) as belonging to three different genera.

In the widely distributed *T. spinifer,* the subspecies *spinifer, hartwegi* and *asper* closely resemble one another; *asper* seems most distinct, whereas *spinifer* and *hartwegi* are terminal populations of an east-west cline in one character. The subspecies *pallidus, guadalupensis* and *emoryi* resemble one another more closely than any resembles any of the subspecies mentioned immediately above; *T. s. pallidus,* however, is annectent. *T. s. pallidus* and *guadalupensis* represent terminal populations of clines in several characters, some of which occur in *emoryi,* but that subspecies is more distinct from *pallidus* and *guadalupensis* than those subspecies are from each other. *T. s. emoryi* is the most variable subspecies. *T. ater,* known only from a restricted area in central Coahuila, is most closely related to *T. s. emoryi,* and possesses some characters judged to represent the attenuation of the geographic cline in *pallidus, guadalupensis* and *emoryi* mentioned above. Some characters of *ater* show alliance to the species *muticus.* Of *T. muticus,* whose geographic range is removed from that of *ater,* there are two subspecies. Four subspecies of *spinifer* (*spinifer, hartwegi, pallidus* and *asper*) intergrade in the Mississippi River drainage of Louisiana; few specimens, however, are typical of *asper.* The subspecies of *muticus* do not show definite evidence of intergradation. To facilitate quick reference, the occurrence of some characters that are shared by, or are approximated in, two or more forms are listed in Table 10. In

Table 10. Frequency of Selected Characters Among Species and Subspecies of Trionyx in North America. Characters of muticus Refer to the Typical Subspecies; Horizontal Dashes Connecting X's Indicate that Computations for Those Subspecies Were Combined; Vertical Dashes Indicate that the Subspecies Is Intermediate Between the Adjacent Subspecies

Characters	Species and subspecies								
	ferox	*spinifer*	*hartwegi*	*asper*	*pallidus*	*guadalupensis*	*emoryi*	*ater*	*muticus*
Juvenal pattern:									
black spots, ocelli		X	X	X					
white dots					X	X	X	X	
Pattern on snout:									
acute angle (reduced in *muticus*)	X	X	X	X	X |				X
triangular					X	X	X	X	
Pattern on side of head:									
contrasting marks	X	X	X	X	X	X |			
non-contrasting marks (distinct stripe in *muticus*)						X	X	X	X
Pattern on limbs of adults:									
contrasting		X	X	X	X	X |			
reduced or absent	X					X	X	X	X
Tuberculation (anterior edge of carapace):									
conical, equilateral		X	X	X	X				
reduced or absent	X					X	X	X	X
Head (PL/HW, fig. 3):									
wide	X			X		X	X	X	
narrow		X	X		X				X
Carapace (CL/CW, fig. 4):									
wide		X	X	X	X	X |			X
narrow	X					X	X	X	
Level of Carapace Width (CL/PCW, fig. 5):									
middle of carapace	X	X	X	X					X
farther posteriorly					X	X	X	X	
Snout (HW/SL, fig. 6):									
long		X—	—X	X	X— |	—X |			X
short	X				X—	—X	X	X	

addition to external characters, some ratios emphasize the clinal relationship between *T. s. pallidus, guadalupensis,* and *emoryi* mentioned above. Of especial interest is the frequent resemblance of those subspecies and *T. ater* to *T. ferox* (dorsal pattern on limbs of adults, reduction in anterior tuberculation, wide head, narrow carapace, and short snout), and the less marked resemblance of *T. muticus* to *T. ferox;* not shown in Table 10 is the resemblance of *ferox* to *T. muticus calvatus* in having thick, black-bordered postocular stripes. Some populations of *T. s. emoryi* resemble *T. muticus* in the corresponding size at sexual maturity and in having well-developed plastral callosities. It is notable that the occurrence of *ater,* and to a lesser extent that of *T. s. emoryi,* which resembles *ferox* (and *muticus*), is in the southwestern United States and northern México.

Fossils

The known occurrence of fossil trionychids throughout the world indicates a former distribution more widespread than the family has today; the principal difference in the former and present distributions is the lack of living softshells in Europe.

I have not studied in detail the many fossil remains but such examination as I have made of them suggests that many of the characters used as a basis for distinguishing fossil forms in North America are subject to individual variation or are of no diagnostic value in the living species (Hummel, 1929:769). Knowledge of the variation in the living species of the Old World would aid in adequately appraising the North American fossils. Some osteological characters of the three living American species (excluding *ater*) together with data on variation within a given species are mentioned below. Some differences in skulls of the three species already were mentioned in the section "Osteological Characters." Because most fossil remains are those of the carapace and plastron, attention is here given to those structures.

Widened alveolar surfaces of jaws.—An ontogenetic variation affecting large skulls of *T. ferox* and some individuals of *T. spinifer asper;* presumably confined to females. Of especial interest is its presence in some populations of *asper* that are not otherwise distinguishable (external characters) from the rest of the individuals comprising that subspecies.

Sculpturing.—No differences in pattern (generally of anastomosing ridges) on carapace or plastron; fineness or coarseness seemingly correlated with size; frequency and kind (knoblike or ridgelike) of bony prominences on carapace variable; bony prominences confined to species *spinifer* and *ferox,* occurring principally on large females.

Fontanelles of carapace.—Closure more or less correlated with increasing size, although much variation noted between individuals of same size; small individuals have fontanelles confluent (medially), thus separating nuchal from contact with first neural and first pair of pleurals.

Number and arrangement of neurals and pleurals.—Neurals number six to nine, usually seven or eight; pleurals number seven or eight pairs, and may or may not be in contact with each other posteriorly; eighth pair of pleurals when present reduced, never contacting seventh neural; arrangement posteriorly variable (see Fig. 16 and Tab. 5).

Plastral callosities.—Increase in size with advancing age causing corresponding reduction in size of plastral vacuity; relatively best developed in *muticus* (all elements touching medially on KU 41380 leaving no plastral vacuity); probably no callosities on preplastra or epiplastron of *ferox;* callosity on epiplastron of *spinifer* not covering entire surface (as it may in *muticus*).

Epiplastron.—Obtusely-angled (greater than 90 degrees) in *muticus;* acutely-angled (90 degrees or less) in *ferox* and *spinifer.*

Hyo-hypoplastral suture.—Usually present, but occasionally absent, in all species.

The fossil turtles of North America have been treated monographically by Hay (1908), who apportioned fossil trionychid remains into eight genera (three living) of two families. Recently, Romer (1956:514) relegated all trionychid fossils to the genus *Trionyx.* Characters, as gleaned from Hay's synopsis (*op. cit.*:465-548, Pls. 85-113), that seem especially worthy of taxonomic consideration are: (1) The presence of a preneural, which is not known to occur in the living American species (seemingly the preneural is fused with the first neural and represents the elongate first neural in living species); (2) The large eighth pair of pleurals, especially when they contact the seventh neural; (3) The thickness of the costal plates, a condition probably correlated with the size of some fossils, which are larger than any living species (for example, Hay, *op. cit.*:518, mentioned the greatest dimension of a nuchal bone as approximately 300 mm.).

The approximate extent of the known horizontal distribution of fossils is indicated in Figure 24. A comparison of known localities of fossils and the distribution of living softshells (introduced population of *T. s. emoryi* in Colorado River drainage omitted) shows that the distribution was more widespread in former times. Localities of fossils are centered on the Atlantic Coast from New Jersey to North Carolina and in the Rocky Mountain-Great Plains region from Alberta and Saskatchewan to northwestern New Mexico; the oldest fossils, which occur in each region, are found in Upper Cretaceous deposits. Many fossils occur in marine and brackish water deposits. Most localities depicted on the map are mentioned by Hay (1908:36-37, 465-548). Other localities included on the map are in southern Alberta (Russell, 1929:164; 1930:27; Sternberg, 1926:104), southern Saskatchewan (Russell, 1934:109), northern South Dakota (Hay, 1910:324), central Utah (Gilmore, 1946), western Colorado (Schmidt, 1945), southwestern Kansas (Galbreath, 1948:284), southeastern Texas (Hay *in* Stejneger, 1944: 65), southern California (Brattstrom, 1958:5), and northeastern Coahuila, México (Mullerried, 1943:623). Hay's record of the living *Platypeltis* (= *Trionyx*) *ferox* and other remains from the Peace Creek formation in Hillsborough County, Florida (*op. cit.*: 548), presumably is the same record mentioned by Pope (1949: 305).

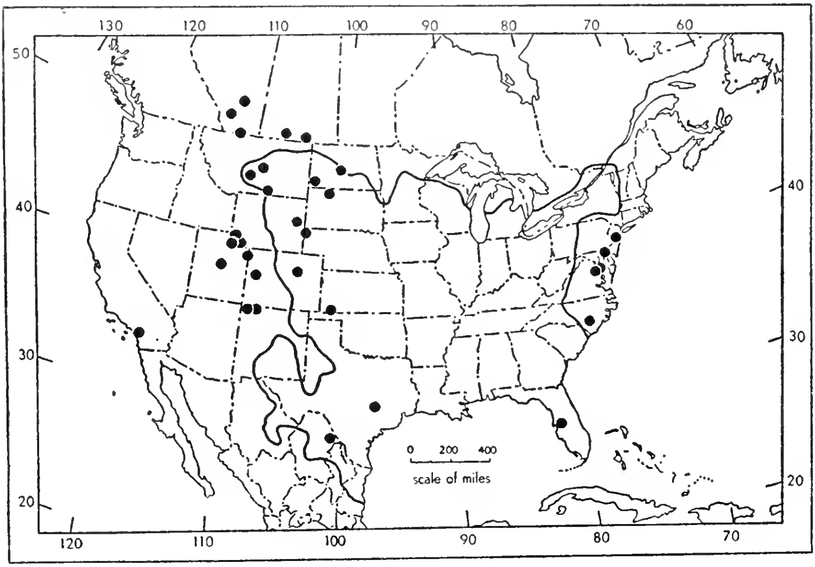


Fig. 24. Geographic distribution of Recent soft-shelled turtles (bordered by heavy black line) and fossil trionychids (black circles) in North America. The introduced population of *T. s. emoryi* in the southwestern United States is not shown.

Ameghino (in Hay, *op. cit.*:35) recorded specimens of a trionychid from the Cretaceous of Patagonia, a record that, at present, cannot be accepted (Simpson, 1943:423). Mullerried (*loc. cit.*) also mentioned some trionychid remains that were housed in Tuxtla Gutierrez, Chiapas, México, (material now lost), but their geographical provenance was unknown. The former extent of range southward is not known; it is improbable that trionychids occurred in South America (Simpson, 1943:423).

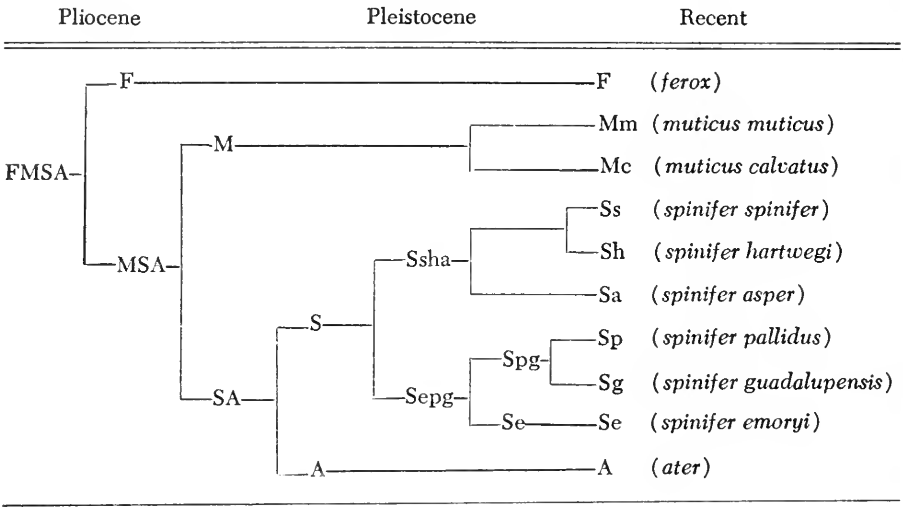
Phylogeny

The occurrence of *T. ferox* in Florida and the suggestion of *ferox*-like characters in turtles from southwestern Texas and northern Mexico presents a distributional pattern that resembles the disjunct ranges of many other pairs of closely related taxa. The clear-water ponds in central Coahuila, which are inhabited by *ater*, correspond to aquatic habitats supporting *ferox* in Florida. The splitting of the geographic range into eastern and western parts possibly resulted from a southward shift of colder climates in glacial stages of the Pleistocene, or from the development of an intervening arid region in the late Miocene and Pliocene (see discussions in Martin and Harrell, 1957, and Blair, 1959). An initial separation of range by an arid environment in the Pliocene may have been terminated by the colder climates in the Pleistocene.

The degree of morphological difference between *ferox* and the forms in southwestern Texas and northern México, suggests that the time of separation antedated the Pleistocene.

Trionychid turtles may have traversed the Bering land bridge between Asia and North America in late Mesozoic times for they occur as fossils on the Atlantic Coast and in the Rocky Mountain-Great Plains region in Upper Cretaceous deposits. Shallow, inland seas may have afforded no barrier to the dispersal of softshells which presumably were tolerant of saline waters. The orogeny and volcanic action with subsequent erosion and sedimentation of the Rocky Mountain system, which was later accompanied by drier climates, tended to obliterate suitable habitats in the western United States; softshells persisted at least until the Upper Eocene on the west coast (Brattstrom, 1958:5). The factors responsible for the disappearance of softshells on the Atlantic Coast probably were related to the glacial advances in the Pleistocene; the most recent fossils known occur in Miocene deposits.

The relationships of the living species and subspecies were probably correlated with geologic change in aquatic environments and drainage patterns. These changes probably included stream capture, flooding, drought, uplifting and planation. A hypothetical, evolutionary history is presented in the phylogenetic diagram where letter symbols represent species and subspecies, and grouped symbols (referred to in subsequent paragraphs) represent ancestral stocks.



An arid environment in the central and southern United States and northern Mexico may have increased in area especially southward from Miocene times into the Pliocene (Dorf, 1959:189, 191). The combination of physiographic changes and aridity, which modified the mesic, essentially continuous, aquatic habitats, may have isolated and aided in the differentiation of the *ferox*, *muticus* and *spinifer* stocks. Encroachment of the Eocene seas, the maximal extent of which corresponded to the Gulf Coastal Plain and included a northerly extension as far as Cairo in southern Illinois (Mississippi embayment), possibly was an initial barrier isolating the *ferox* stock of the east.

In the late Miocene or early Pliocene, the MSA (*muticus-spinifer-ater*) stock presumably occupied a large region of the central United States, which extended southward into northern México and along the Gulf Coast at least as far as Alabama. Farther eastward, the *ferox* stock was isolated in more mesic, probably swampy, marshy habitats.

Later, in the southwestern part of the range of the MSA stock (southern Texas and northern México), the SA and *muticus* stocks were separated. The *muticus* stock occurred to the northeastward, and presumably no farther south than the area included within the present drainage basin of the Colorado River. Southward, the SA stock was isolated into several populations that are today represented by *ater* and *T. s. emoryi*, the most variable subspecies; the distribution of the most distinctive population of *emoryi* indicates a former isolated inland drainage. The multiple fragmentation of the SA stock presumably terminated by the end of the Pliocene. The progenitors of *T. ater* probably closely resembled *ferox*. *Trionyx ater* and *T. ferox* resemble each other morphologically and in habitat. Therefore, the progenitors of *ater* are considered to have undergone comparatively little differentiation.

The *spinifer* stock, occurring principally in the area included within the present drainage basin of the Río Grande, extended its geographic range eastward and became sympatric with *muticus* and *ferox*. An expansion of range necessarily demands more mesic conditions; these were perhaps afforded by the pluvials (wet, rainy ages) that were coincident with the glacial periods in the Pleistocene (Antevs, 1948:168). The pluvials permitted the isolated populations of the *spinifer* stock to unite, and permitted that stock to extend its range eastward. The concurrent continental glaciation permitted the *spinifer* stock to extend its range eastward only in a belt approximately 300 miles wide along the Gulf Coast, and also displaced the ranges of *ferox* and *muticus* to southern latitudes. Perhaps *ferox* was less tolerant of decreased temperatures or changes in habitat than was the *spinifer* stock but, for some unknown reason, *ferox* did not extend its range westward. Because *T. ater* closely resembles *T. s. emoryi*, continued isolation of *ater* since the beginning of the Pleistocene seems unlikely and *ater* may have been reunited in subsequent pluvial periods with the *spinifer* (*emoryi*) stock. A climatic fluctuation between relatively wet and dry periods is corroborated by studies of soil profiles in Trans-Pecos Texas (Bryan and Albritton, 1943).

The separation of the range of *spinifer* in the general region of western Louisiana, resulting in the differentiation of the *spinifer* group of subspecies to the east and the *emoryi* group of subspecies to the west, and the differentiation of *T. s. asper* and *T. m. calvatus*, both having corresponding western limits of distribution (Mississippi River drainage), are associated with the activities of the Mississippi River and its floodplain. The combined effects of the pluvials and interpluvials seem responsible for changes in the lower Mississippi Valley. Great volumes of summer melt-water in the glacial stages greatly increased the breadth of the channel of the lower Mississippi River (corresponding to the northern extent of the Mississippi embayment; Hobbs, 1950), and this, coupled with the encroachment of Pleistocene seas (especially in the Mississippi embayment) in the interglacial periods, perhaps separated populations eastward represented today by *T. m. calvatus* and *T. s. asper*. The *spinifer-hartwegi* stock probably developed in southern Louisiana in association with the meandering of the Mississippi River and its tributaries, and its broad alluvial plain. The biota of that plain differed from that adjacent to the east or west (see discussion in Viosca, 1944) and constituted a barrier, of a sort, to free communication between the east and west. Westward the *emoryi* group of subspecies differentiated, its eastern limit probably being the Red River, which followed its own course to the Gulf along the lowlands on the west side of the Mississippi Valley and did not empty directly into the Mississippi until Recent times (Holland, 1944:20). There was not an equally-marked, corresponding separation of the range of *muticus*. However, the juvenal pattern of the subspecies *muticus* that inhabits the Gulf Coast streams is slightly different (having less short lines) from that of *muticus* elsewhere.

The Río Grande (inhabited by *emoryi*) presumably had its own exit to the Gulf whereas rivers westward to (and including) the Red River (inhabited by *pallidus-guadalupensis* cline) probably were joined near their mouths forming a large drainage system. Hubbs (1957:93) pointed out that the Río Grande-Nueces divide also limits a large number of species of fish. The differentiation of *pallidus* and *guadalupensis* is possibly due to a difference in the salt content of waters that drain the Edward's Plateau (see page 547), or to isolation of those subspecies in separate drainage systems that had their own exits to the Gulf.

In the lower Mississippi drainage, the *spinifer-hartwegi* stock extended its range northward following the retreat of the last glacial stage, and differentiated into those two subspecies in the upper Mississippi drainage and Great Lakes-St. Lawrence drainage system.

I have seen one specimen (UMMZ 59198) from the eastern part of the Tennessee drainage (inhabited by *T. s. spinifer*) that resembles *T. s. asper* (occupying the Gulf Coast drainages of the southeast). This resemblance tends to support the thesis of a former confluence of the Coosa (Alabama River system) and Tennessee drainages as believed by some malacologists to explain resemblances in molluscan fauna and as corroborated by physiographical evidence (see discussion in van der Schalie, 1945).

The Importance of the Study of Turtle Populations in Relation to the History of River Systems

In the Río Grande drainage the geographic distribution of the population of *emoryi* having orange color in males is approximately the same as that of *Pseudemys scripta gaigeae;* the corresponding distributions suggest that a part of the Río Grande drainage consisting of the Río Conchos in Chihuahua and the Big Bend region of Texas was isolated in former times. Accordingly, the known aquatic chelonian fauna in the basin of Cuatro Ciénegas in central Coahuila, México, is endemic (except *T. s. emoryi*). And the coincidence of the geographic ranges of *T. muticus calvatus* and *Graptemys pulchra* in the southeast suggest a former association of the included (Pearl to Escambia) river systems. The occurrence of *T. s. pallidus* in the Red River drainage indicates that the Red River was formerly associated with the Gulf Coast streams of eastern Texas and western Louisiana (inhabited by *pallidus*) and not with the Mississippi River drainage. The lower Mississippi River valley forms a prominent barrier to the eastern and western dispersal of many kinds of species and subspecies of turtles. *T. m. calvatus* and *T. s. asper*, which occur in rivers of the Gulf Coast drainage east of the Mississippi, are well-differentiated subspecies showing little or no evidence of intergradation with their relatives in the Mississippi River. The large faunal break provided by the Mississippi River would seem to indicate greater age for that river than for other rivers of the Gulf Coast drainage.

A comparison of the distributions of *Trionyx* and *Graptemys* in Texas suggests a faunal break between the drainage systems of the Brazos and Colorado rivers. *Graptemys versa* occurs in the Colorado and Guadalupe-San Antonio drainages. To my knowledge *versa* hitherto has not been recorded from the latter drainage system. I have seen one specimen of *Graptemys* (custody of Gerald Raun, University of Texas) from the Guadalupe River drainage, which I judge to be representative of *versa*, and Olson (1959:48) has reported *Graptemys* (probably *versa*) in the San Antonio River. The distribution of *G. versa* parallels in a general way, the distribution of *T. s. guadalupensis*. *G. kohni* and *T. s. pallidus* occur in the Brazos River and eastward. Also, it is notable that the population of *T. m. muticus* occurring in the Colorado River drainage differs slightly (more black pigmentation) from the same subspecies in the adjacent Brazos River system.

There is much difference in the patterns of distribution and degree of differentiation of different genera of aquatic turtles in the eastern United States. Tinkle (1958:41-43, Figs. 49-55) concluded that a general resemblance in the patterns of distribution of the different genera of turtles was evidence that the rates of evolution were essentially the same, assuming that each genus had had a similar time interval for differentiation (*op. cit.*:42). If this is true, corresponding patterns of distribution might indicate the same relative age of the population of turtles concerned. Generally, the genera of turtles that on morphological grounds are considered the oldest and most primitive (*Macroclemys, Chelydra*) show less differentiation into species and subspecies than those considered younger and more recently evolved (*Graptemys, Pseudemys*). In the genus *Graptemys,* much differentiation occurs in the geologically, recently formed, Gulf Coast drainage systems of the southeastern United States. It would seem then, that faster rates of differentiation denote more recent genera, whereas older genera are endowed with a "genetic senility" and are less subject to change.

Evidence of the relative age of two genera of turtles, as suggested by their degree of differentiation into minor taxa, and the degree of difference between populations of two genera that inhabit adjacent drainage systems, may indicate the relative ages of particular river systems. For example, the slight resemblance of *G. versa* to *kohni* and the close resemblance of *T. s. guadalupensis* to *pallidus* in Texas may reflect the age of the genus *Trionyx* and the youth of the genus *Graptemys.* Remembering that the genus *Graptemys* is relatively recently evolved and assuming *G. versa* to be the most primitive and ancestral species of the genus (at least it is monotypic, the most aberrant species, and unlike any other species of the genus), it seems logical to suppose that the physiographic changes responsible for the Colorado-Brazos divide and the isolation of *versa* occurred early in the evolutionary history of the genus *Graptemys.* The degree of differentiation of *Trionyx* suggests that that genus is, comparatively, much older, and that the same physiographic changes responsible for the Colorado-Brazos divide and differentiation of the subspecies *pallidus* and *guadalupensis* occurred late in the evolutionary history of the genus *Trionyx.*

In general, patterns of distribution of turtle populations support physiographic evidence concerning changes in stream confluence and relative age of river systems.

SUMMARY

In North America, soft-shelled turtles (genus *Trionyx*) occur in northern México, the eastern two-thirds of the United States, and extreme southeastern Canada. The genus fits the well-known Sino-American distributional pattern. In North America there are four species. Three (*ferox, spinifer* and *muticus*) are well-differentiated and one (*ater*) is not well-differentiated from *spinifer.* Characters of taxonomic worth are provided by the following: size; proportions of snout, head and shell; pattern on carapace, snout, side of head, and limbs; tuberculation; sizes of parts of skull; number of parts of carapaces; and, shape and number of some parts of plastra. Many features show geographical gradients or clines. *T. ferox* is the largest species and *muticus* is the smallest. Females of all species are larger than males. With increasing size of individual, the juvenal pattern is replaced by a mottled and blotched pattern in females of all species; adult males of *spinifer* retain a conspicuous juvenal pattern, whereas the juvenal pattern is sometimes obscured or lost on those of *ferox* and *muticus.* The elongation of the preanal region in all males, and the acquisition of a "sandpapery" carapace in males of *spinifer* occur at sexual maturity. There is a marked secondary sexual difference in coloration in a population of *T. s. emoryi* (side of head bright orange in males and yellow in females). The sex of many hatchlings of *T. s. asper* can be distinguished by the pattern on the carapace. Slight ontogenetic variation occurs in some proportional measurements. Large skulls of *ferox* and some *asper* (those in Atlantic Coast drainages) have expanded crushing surfaces on the jaws. Considering osteological characters, *muticus* is most distinct; there is less difference between *ferox* and *spinifer* than between those species and *muticus.*

T. ferox is monotypic, confined to the southeastern United States, and resembles Old World softshells more than it does any American species. The northern part of the geographic range of *ferox* overlaps that of *T. s. asper;* there, the two species are ecologically isolated. *T. spinifer* is polytypic, has the largest geographic range, and is composed of six subspecies, of which two are described as new (*pallidus* and *guadalupensis*). The subspecies are divisible into two groups. One, the *spinifer* group (*spinifer, hartwegi* and *asper*) is recognized by a juvenal pattern having black spots or ocelli; *asper* is the most distinctive and shows little evidence of intergradation in the lower Mississippi River drainage with the *spinifer-hartwegi* complex, which, northward, is differentiated into two subspecies in which there is an east-west cline in size of the ocelli on the carapace. The *emoryi* group (*pallidus, guadalupensis, emoryi*) is recognized by a pattern of white spots; *emoryi* is most distinctive. Each of several characters behaves as a cline if traced from east to west through the three subspecies. *T. s. pallidus* intergrades with the *spinifer-hartwegi* complex in the lower Mississippi River drainage. *T. s. emoryi* is the most variable subspecies; in its most notable population the males have orange coloration. *T. s. emoryi* has been introduced into the Colorado River drainage of Arizona. *T. ater* most closely resembles *T. s. emoryi,* but shows alliance with *T. muticus* and *T. ferox.* *T. ater* is confined to ponds of crystal-clear water in central Coahuila, México. *T. muticus* is completely sympatric with *spinifer,* and is composed of two subspecies (*muticus* and *calvatus*). *T. m. calvatus* shows no evidence of intergradation in the lower Mississippi River drainage with *T. m. muticus,* corresponding somewhat to the relationship of *T. s. asper* with the intergradient population of *T. spinifer* in the Mississippi River.

Softshells have pharyngeal respiration and probably are incapacitated by rotenone. *T. ferox* and the subspecies of *spinifer* occur in a wide variety of fresh-water habitats; *muticus* is more nearly restricted to running water (especially in the northern parts of its range) than *spinifer,* and may be less vagile than *spinifer.* *T. ferox* is more tolerant of marine and brackish waters than are *muticus* or *spinifer.* Small size and pallid coloration seem correlated with arid environments. The largest species (*ferox*) and the smallest population of *spinifer* (resembling *muticus*) both occur in the southernmost part of the range of the genus. Diurnal habits include basking on shores or débris in water, floating at the surface, procuring food, and burrowing in shallow and deep water (no observations for *spinifer* and *muticus* in deep water). Softshells are principally carnivorous; the food consists mostly of crawfish and insects; there is evidence of cannibalism involving predation on first- and second-year-old turtles. The capture of food is triggered primarily by movement of prey; sight seems to be more important than smell to *Trionyx* in capturing food. There is no indication of a food preference between species; enlarged crushing surfaces of jaws in some *ferox* and *asper* may be an adaptation for feeding on mollusks. Schools of fish are reported to follow softshells, and presumably acquire food that is dislodged by the grubbing and scurrying of the turtles on the bottom. Softshells are wary. They are good swimmers, and travel rapidly on land. The depressed body is an adaptation for burrowing and concealment. Permanent growths of algae do not occur on the dorsal surface of softshells. There is evidence of some nocturnal activity, and a general parallel in habits between trionychids and chelydrids. Softshells sometimes move overland; they move little in aquatic habitats. The normal annual period of activity of *spinifer* in latitudes 40° to 43° is approximately five months from April into September, depending on the weather; they hibernate under a shallow covering of mud in deep water. The southernmost populations may be active throughout the year.

Males of *spinifer* are sexually mature when the plastron is 9.0 to 10.0 centimeters in length (some when 8.0 long), whereas those of *muticus* are sexually mature at 8.0 to 9.0 centimeters. In the mentioned size range, the smaller adult males are probably in their fourth growing season, and the larger males in their fifth. Most females of *spinifer* are sexually mature at a plastral length of 18.0 to 20.0 centimeters and are probably in their ninth year; the smaller individuals probably are in their eighth. Females of *muticus* are sexually mature when the plastron is 14.0 to 16.0 centimeters long. Most of these are seven years old but some are only six years old. Some large females contain immature ovaries. The near-maximum length of carapace of *spinifer* is 18 inches, and such turtles are perhaps 60 years old; *ferox* perhaps attains a length of two feet.

T. ferox deposits eggs from late March to mid-July, whereas northern populations of *spinifer* and *muticus* usually deposit theirs from mid-June to mid-July. Sandy sites are preferred for nests, although movement to other sites occurs if the preferred sandy sites are submerged or otherwise rendered unusable. *T. muticus* limits its nest sites to the open areas of sand bars and does not lay inland where it must traverse vegetated areas, as does *spinifer.* Nests of *ferox* and *spinifer* seem to differ from those of *muticus* in being flask-shaped.

The seasonal reproductive potential is perhaps less in northern populations (averaging 20 eggs per clutch and only one clutch per season) than in southern populations (averaging about 10 eggs per clutch, but three clutches per season). Larger females deposit more eggs than smaller females. Eggs laid in northern latitudes are slightly smaller than those laid farther south. In any latitude the incubation period probably is at least 60 days. Hatchlings presumably leave nests at dusk, nighttime or dawn, and may winter over in eggs or nests.

Man is a great enemy of softshells. Predation on eggs probably accounts for most mortality. Physical conditions of the environment (overcrowding of nest sites, inadequate hibernation sites) and probably some kinds of parasitism contribute to mortality. Softshells are eaten locally and sometimes appear in the market of large cities, but over most of their range, there probably is no general demand and no special efforts are made to capture them. Fish, mostly minnows, comprise a small proportion of the diet. There is no evidence that softshells are active predators on any kind of fish, but their known food habits suggest that they compete with game fishes for food. Softshells are scavengers.

Fossil material was not studied in detail. The fossil softshells indicate a more widespread, former distribution. Some osteological characters and their variation in the living species are mentioned as an aid to future workers concerned with an assay of fossil remains. Fossils occur in marine, brackish and fresh-water deposits, and many are much larger than the living species; the oldest American fossils are of Upper Cretaceous age.

The interrelationships of the living species and subspecies suggest that the species *spinifer*, *ater*, and *muticus* are derivatives of a *ferox*-like ancestor, and that they differentiated in North America; most differentiation occurs in southwestern Texas and northern México where characters of some populations indicate alliance with *ferox*. It is hypothesized that aridity in the late Tertiary effected specific differentiation by the modification and isolation of aquatic habitats. Pluvial periods in the Pleistocene provided for confluence of aquatic habitats and expansion of geographic ranges, and coupled with physiographic changes, conceivably caused or enhanced some of the subspecific variation.

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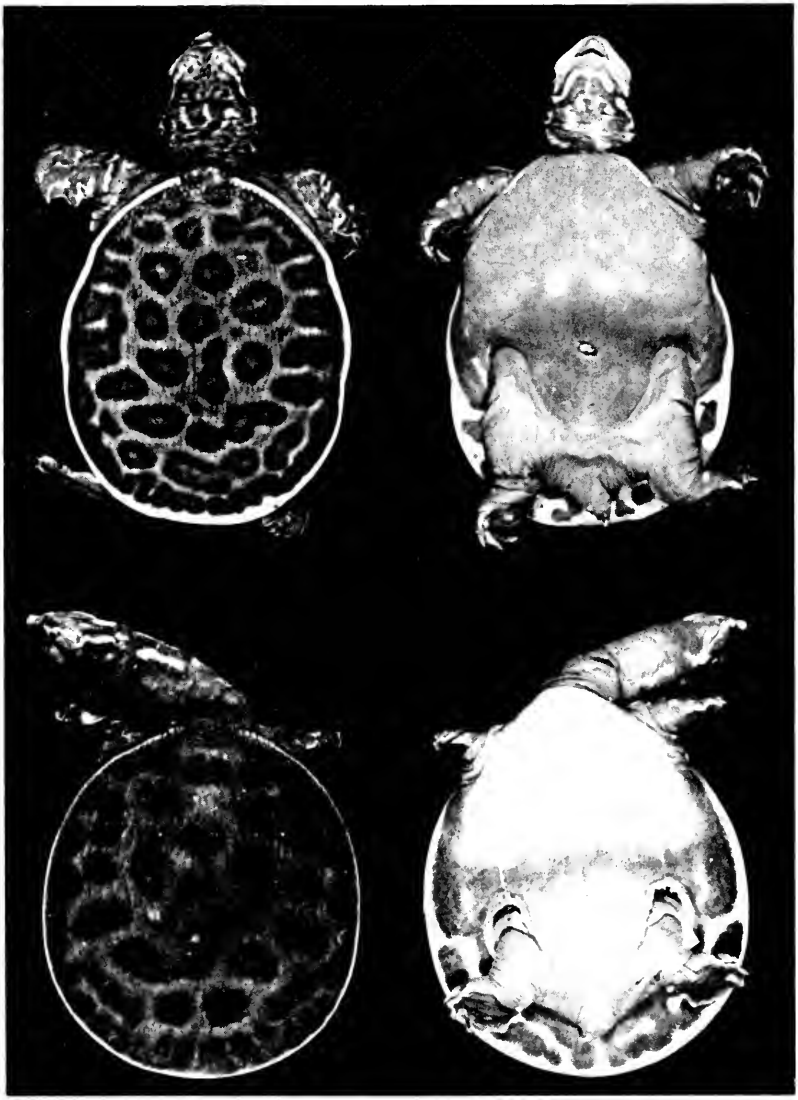
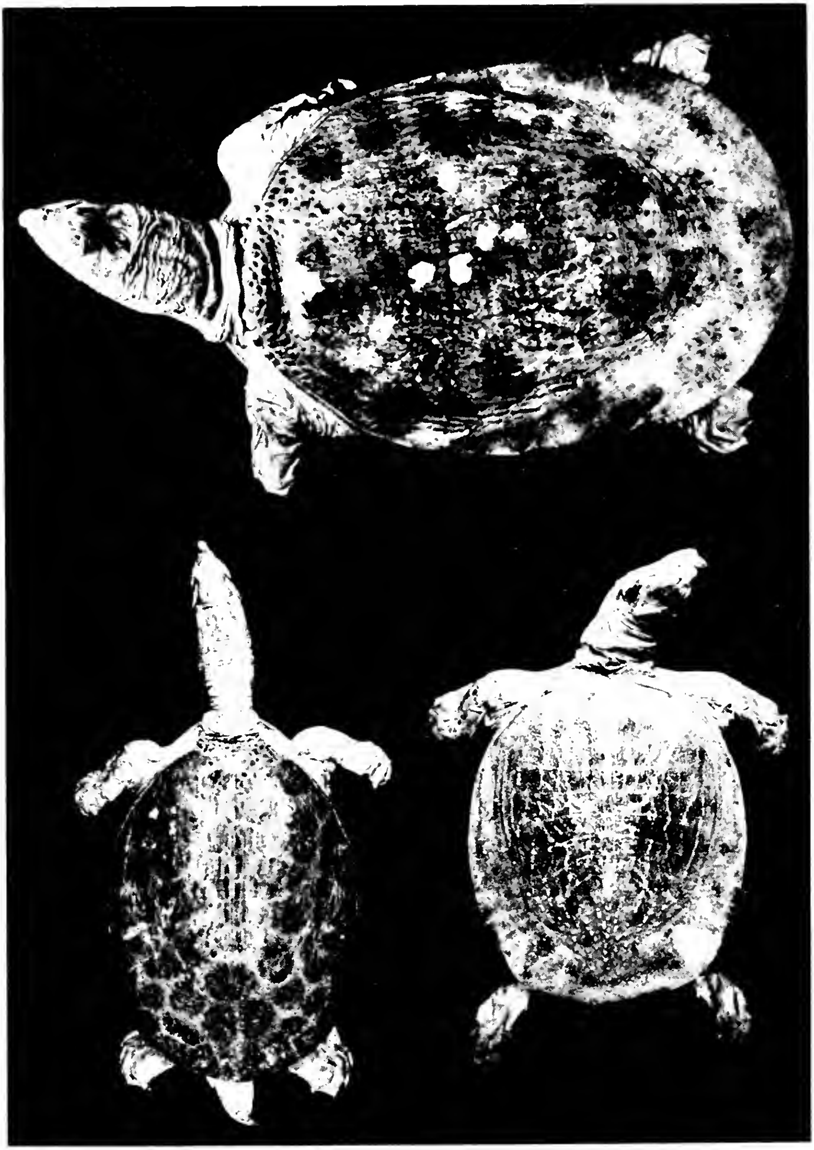
Transmitted June 8, 1961.

PLATE 31



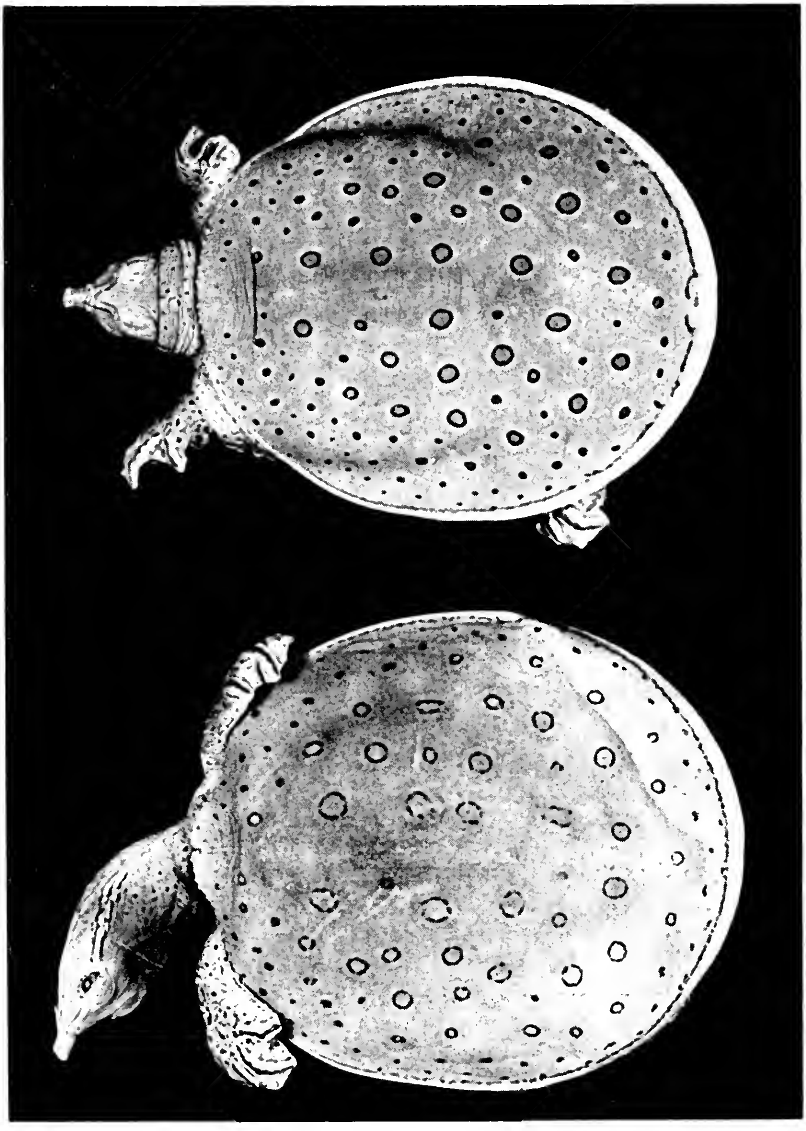
Trionyx ferox, juveniles. *Top*—UMMZ 76755 (× 1) dorsal and ventral views; Lake Griffin, Lake County, Florida. *Bottom*—TU 13960 (× ¾), dorsal and ventral views; Hillsborough River, *ca.* 20 mi. NE Tampa, Hillsborough County, Florida.

PLATE 32



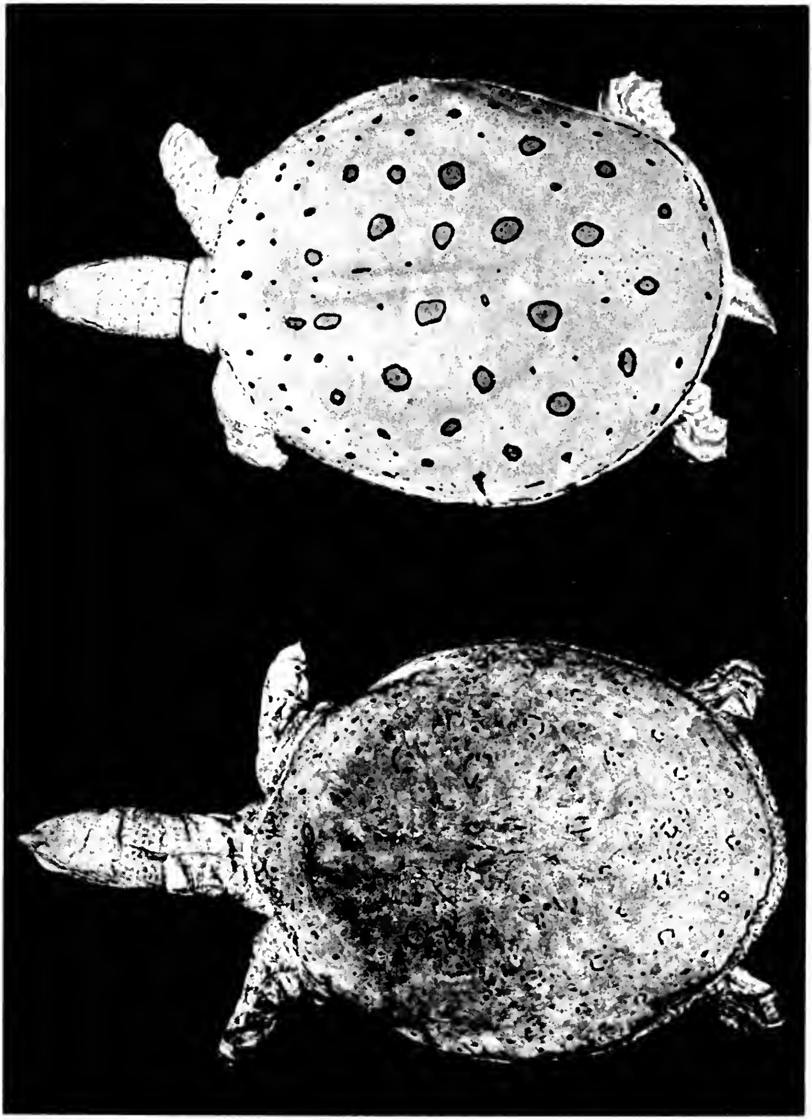
Top—*Trionyx ferox*, female, UMMZ 90010 (× 2/9); east edge Okefinokee Swamp, Charlton County, Georgia. *Bottom*—Left, *Trionyx ferox*, adult male, UMMZ 102276 (× 1/5), 14 mi. SE Punta Gorda, Lee County, Florida; right, *Trionyx sinensis*, female, KU 39417 (× 3/10), 5 mi. ESE Seoul, Korea. All dorsal views; note resemblance of two species in having longitudinal ridging and marginal ridge of carapace.

PLATE 33



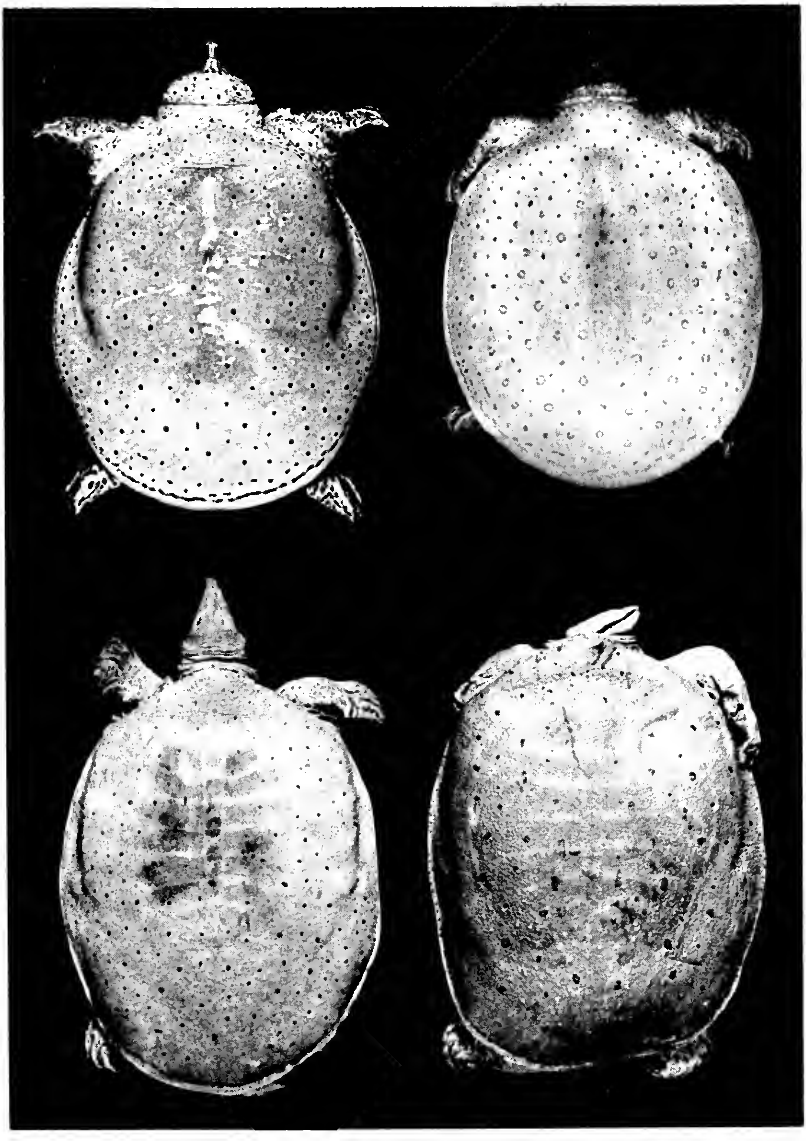
Trionyx spinifer spinifer, juveniles, dorsal views. *Top*—UMMZ 74518 (× $1\frac{2}{5}$); Portage Lake, Washtenaw County, Michigan. *Bottom*—TU 16132 (× $1\frac{1}{5}$); Sevierville, Sevier County, Tennessee.

PLATE 34



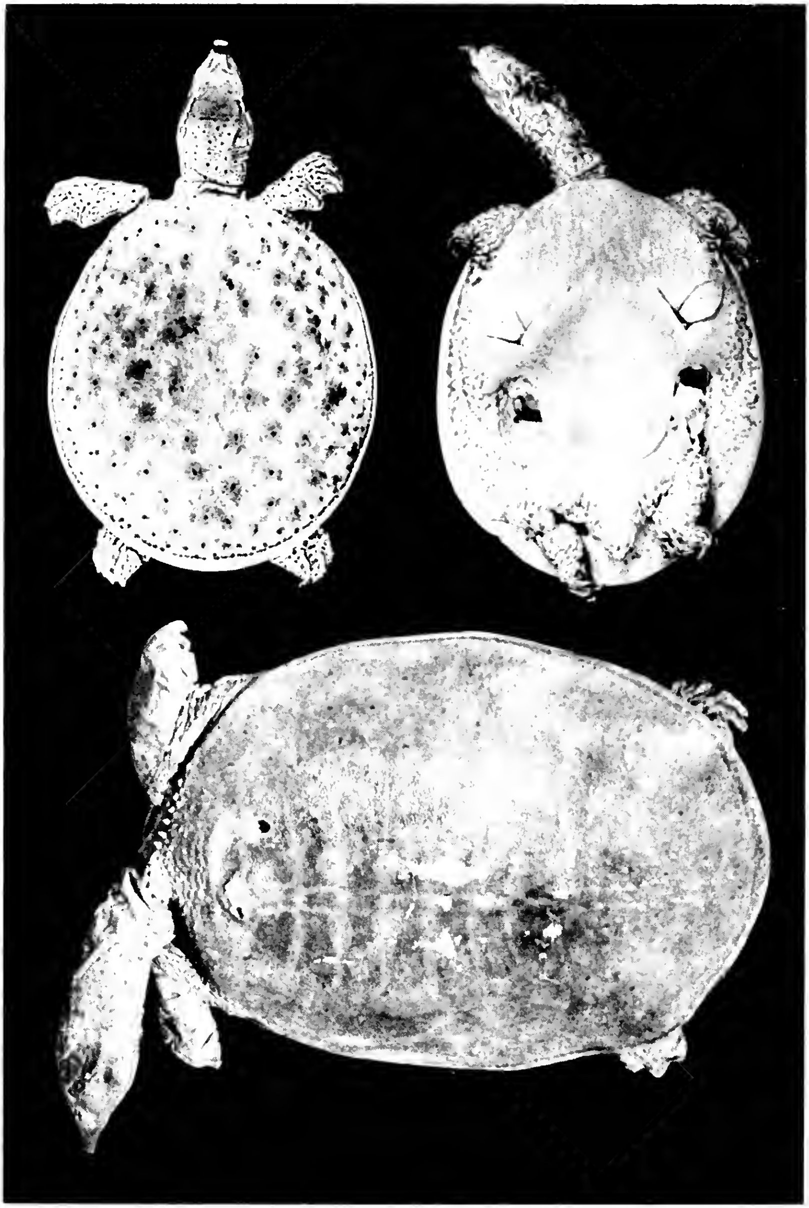
Trionyx spinifer spinifer, dorsal views. *Top*—Adult male, UMMZ 54401 ($\times \frac{3}{7}$), Portage Lake, Livingston County, Michigan. *Bottom*—Female, UMMZ 81699 ($\times \frac{2}{7}$), Ottawa County, Michigan.

PLATE 35

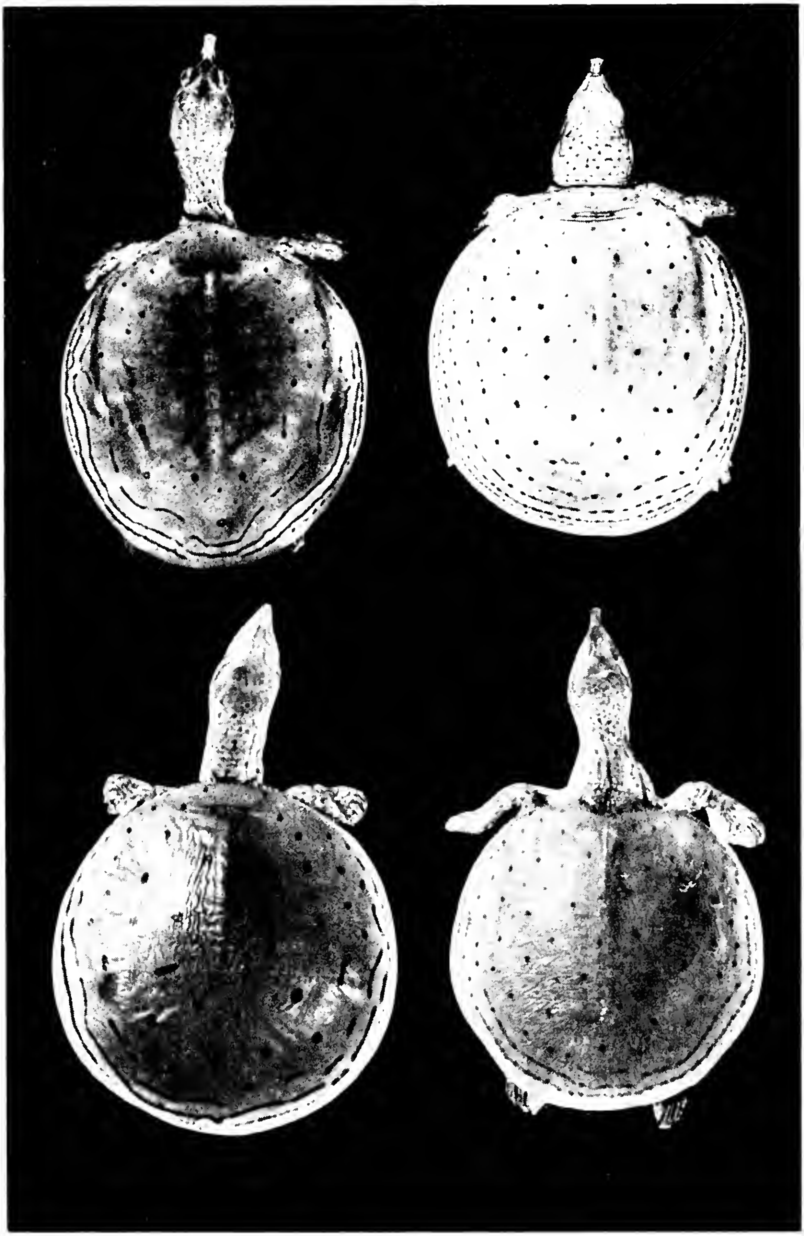


Trionyx spinifer hartwegi, dorsal views. *Top*—Juveniles; left, KU 40210 (× 9/10), 12½ mi. S, 1¼ mi. W Meade, Meade County, Kansas; right, KU 16531 (× 1), Smoky Hill River, 3 mi. SW Elkader, Logan County, Kansas. *Bottom*—Adult Males; left, KU 18385 (× 2/5), Arrington, Comanche County, Kansas; right, KU 3758 (× 3/10), Little Salt Marsh, Stafford County, Kansas.

PLATE 36

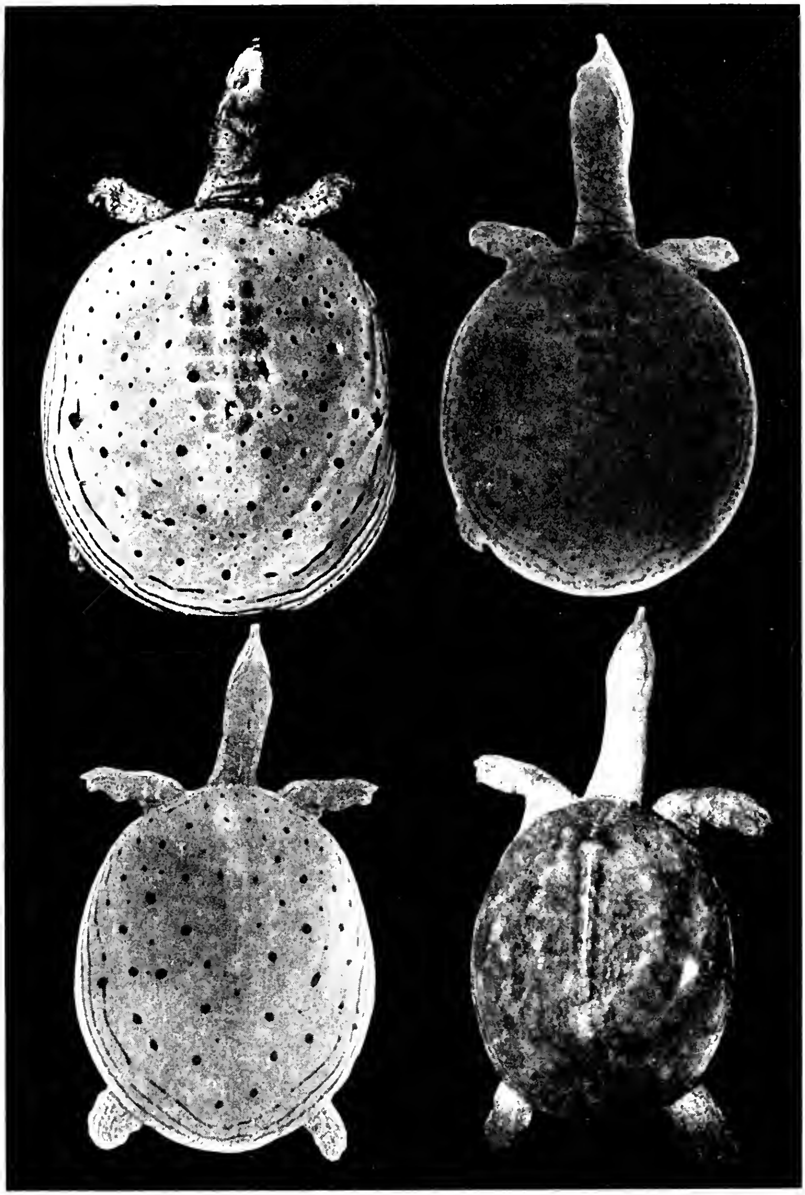


Trionyx spinifer hartwegi. *Top*—Juveniles; left, TU 13885, dorsal view (× 3/4), Little Vian Creek, 1 mi. E Vian, Sequoyah County, Oklahoma; right, KU 3732, ventral view (× 5/7), Independence, Montgomery County, Kansas. *Bottom*—Adult female, TTC 719, dorsal view (× 2/7), 10 mi. S, 2 mi. W Gruver, Hansford County, Texas.



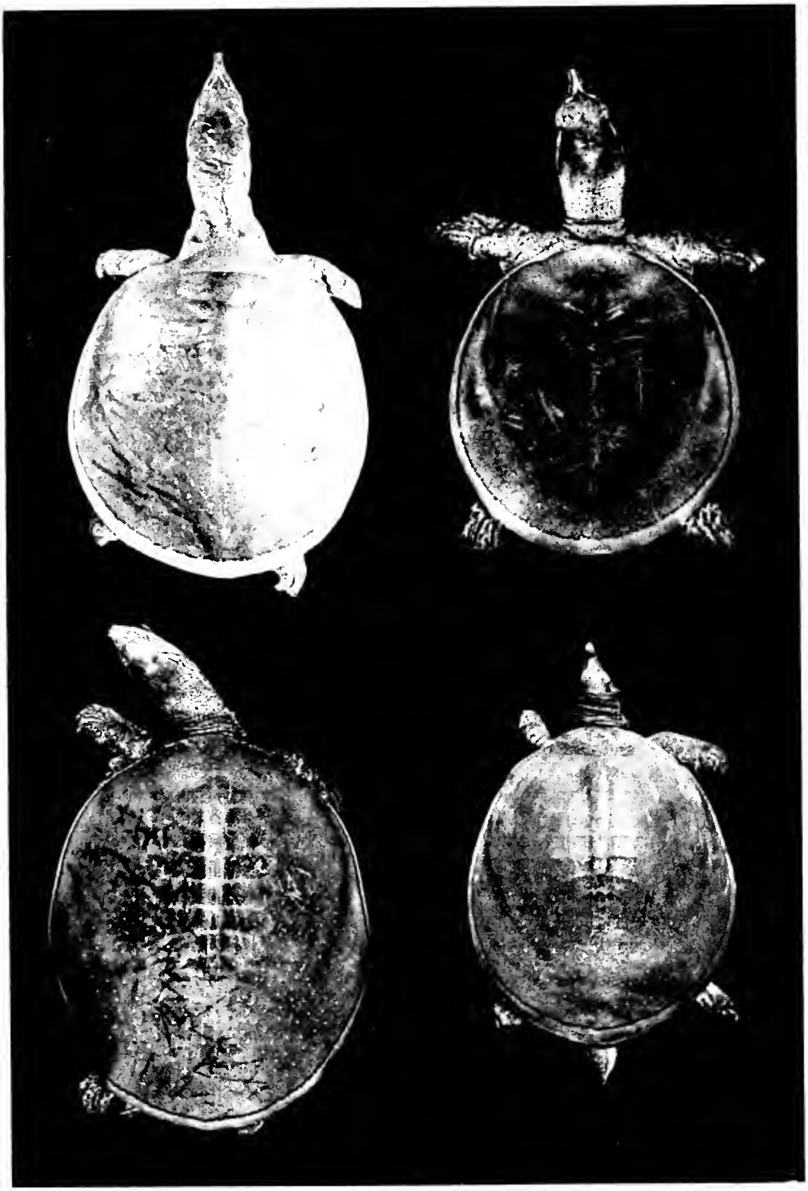
Trionyx spinifer asper, juveniles, dorsal views. *Top*—Left, male, KU 50839 (× 9/10), Flint River, 1½ mi. S Bainbridge, Decatur County, Georgia; right, female, TU 15661 (× 9/10), Blackwater River, 4.3 mi. NW Baker, Okaloosa County, Florida. *Bottom*—Left, male, TU 13623 (× 7/9), Yellow River, 3.1 mi. W Hammond, Tangipahoa Parish, Louisiana; right, female, TU 14362 (× 1/5), Hobolochito Creek, 1 mi. N Picayune, Pearl River County, Mississippi.

PLATE 38



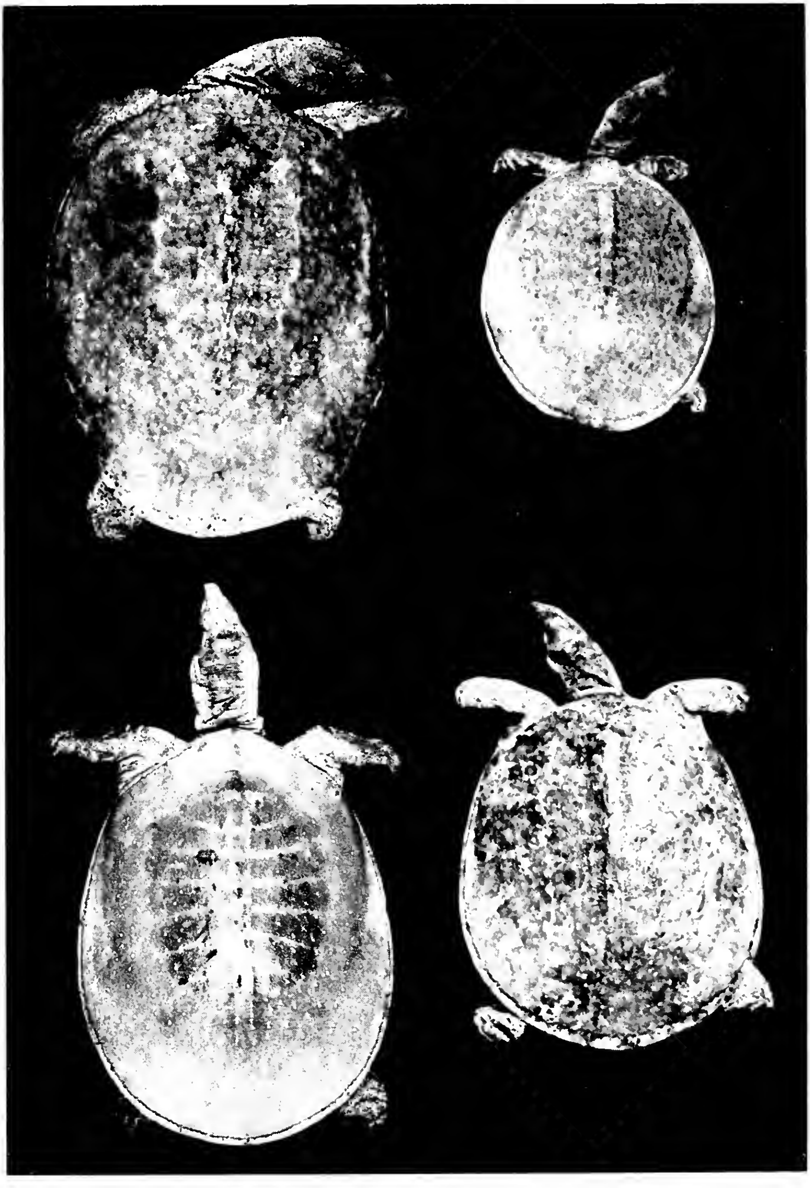
Trionyx spinifer asper, dorsal views. *Top*—Left, adult male, TU 15869 (× ½), Escambia River, 1.2 mi. E Century, Escambia County, Florida; right, female, TU 14673.3 (× ½), Black Warrior River, 17½ mi. SSW Tuscaloosa, Tuscaloosa County, Alabama. *Bottom*—Left, adult male, TU 17117 (× ¼), Pearl River, Varnado, Washington Parish, Louisiana; right, female, TU 16584 (× ⅓), locality same as TU 15869.

PLATE 39



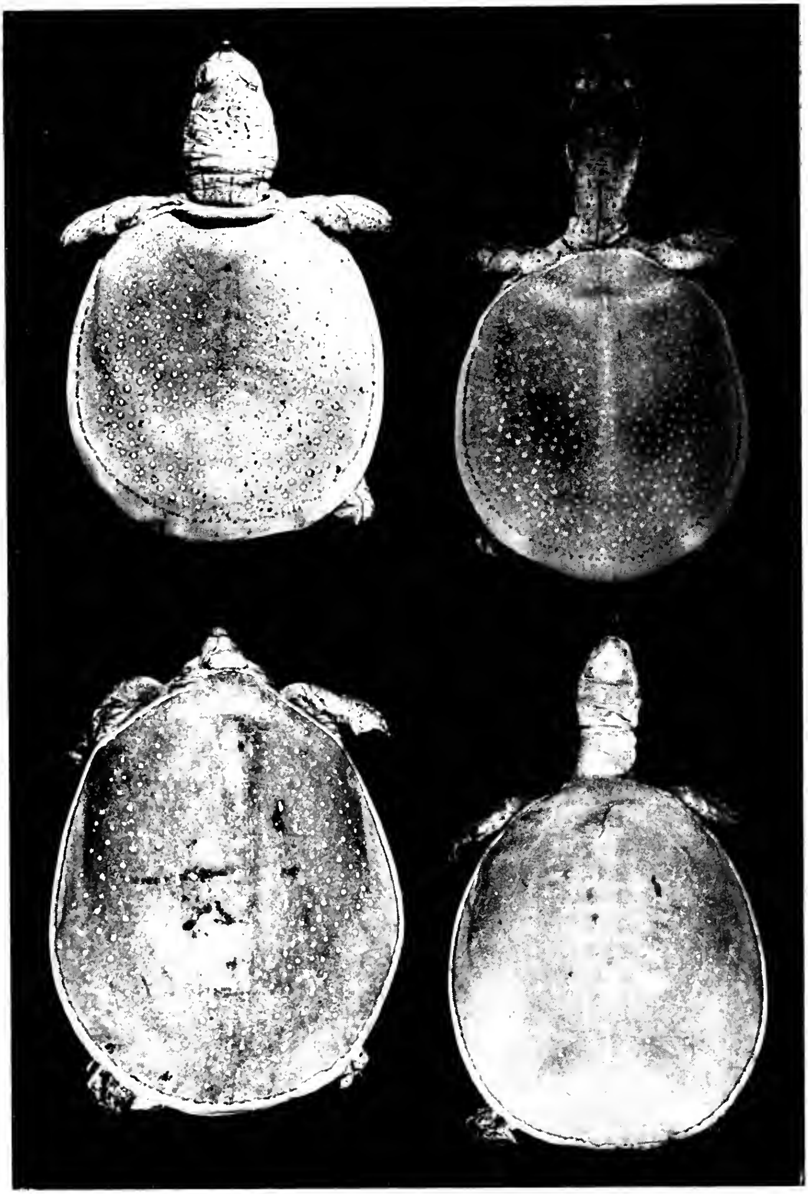
Trionyx spinifer pallidus, new subspecies, dorsal views. *Top*—Juveniles; left, TU 481 (× 2/3), Caddo Lake, Caddo Parish, Louisiana; right, KU 50832 (× 9/10), mouth of Caney Creek, 4 mi. SW Kingston, Marshall County, Oklahoma. *Bottom*—Adult males; left, holotype, TU 484 (× 1/3), locality same as TU 481; right, TU 1122 (× 2/5), Lacassine Refuge, Cameron Parish, Louisiana.

PLATE 40



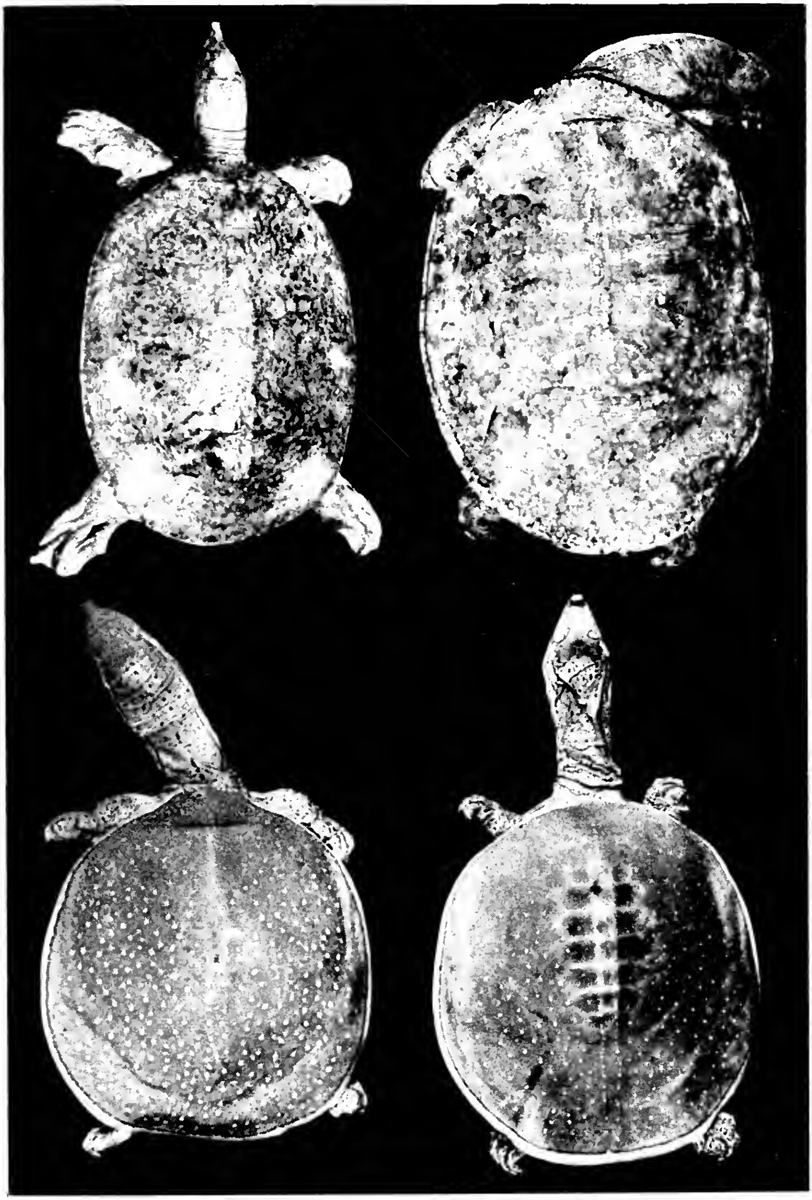
Trionyx spinifer pallidus, new subspecies, dorsal views. *Top*—Females; left, TU 13213 (× 1/4), Sabine River, 8 mi. SW Negreet, Sabine Parish, Louisana; right, TU 13266 (× 2/9), Sabine River, 8 mi. SW Merryville, Beauregard Parish, Louisana. *Bottom*—Left, adult male, SM 2889 (× 1/4), Groveton, Trinity County, Texas; right, female, TU 14402 (× 1/5), Trinity River, near junction with Big Creek, Liberty County, Texas.

PLATE 41



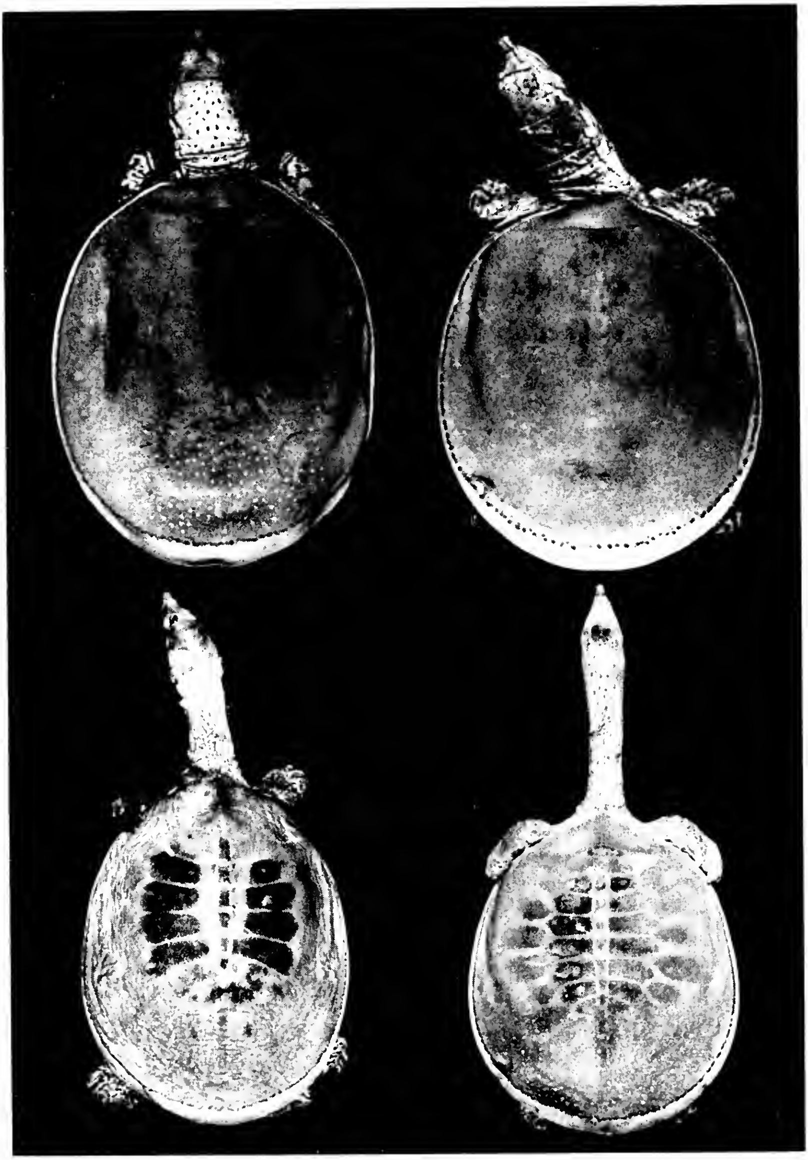
Trionyx spinifer guadalupensis, new subspecies, dorsal views. *Top*—Juveniles; left, ANSP 16717 ($\times$ 1), no data; right, KU 50834 ($\times 1\frac{1}{10}$), Hondo Creek, 4 mi. W Bandera, Bandera County, Texas. *Bottom*—Adult males; left, holotype, UMMZ 89926 ($\times \frac{1}{3}$), 15 mi. NE Tilden, McMullen County, Texas; right, SM 659 ($\times \frac{3}{10}$), Colorado River, near Austin, Travis County, Texas.

PLATE 42



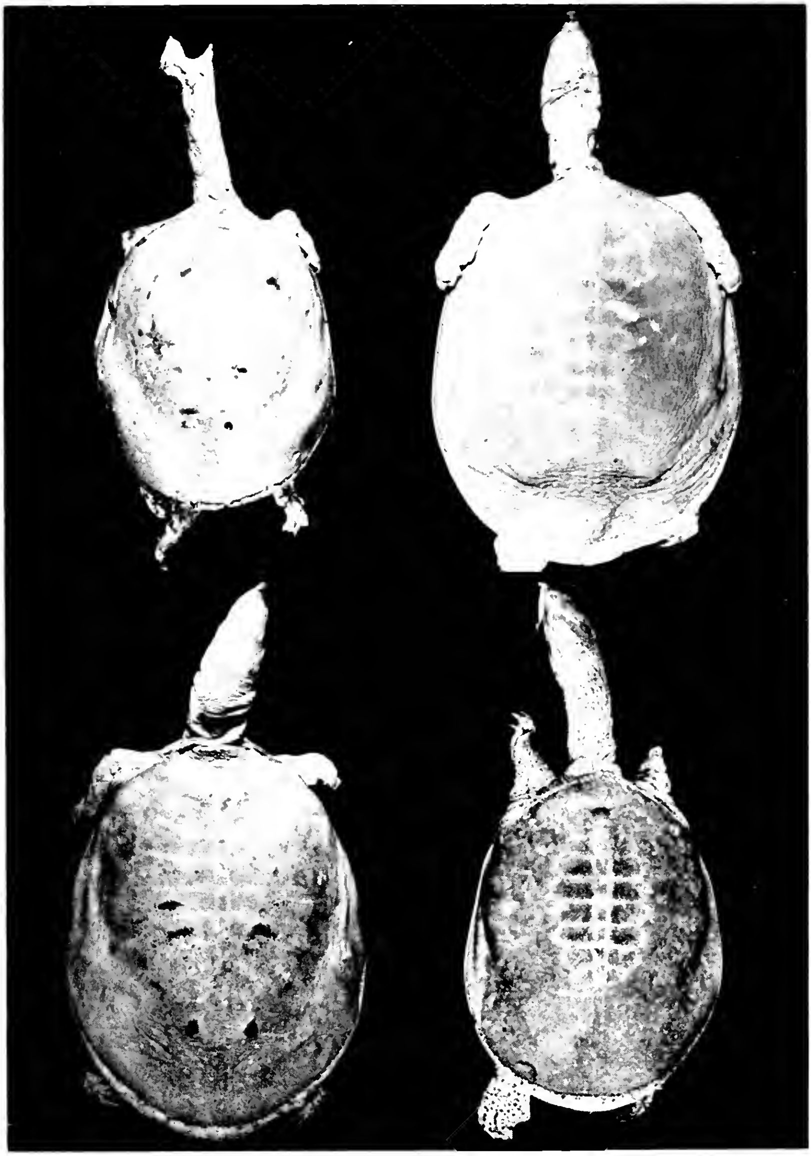
Trionyx spinifer guadalupensis, new subspecies, dorsal views. *Top*—Adult females; left, TU 16036.1 (× 1/5), Llano River, 2 mi. W Llano, Llano County, Texas; right, TU 10160 (× 1/5), Guadalupe River, 9 mi. SE Kerrville, Kerr County, Texas. *Bottom*—Left, female, CM 3118 (× 3/4), Black Bayou, Victoria County, Texas; right, male, TU 14419.6 (× 5/9), San Saba River, 11 mi. NNW San Saba, San Saba County, Texas.

PLATE 43



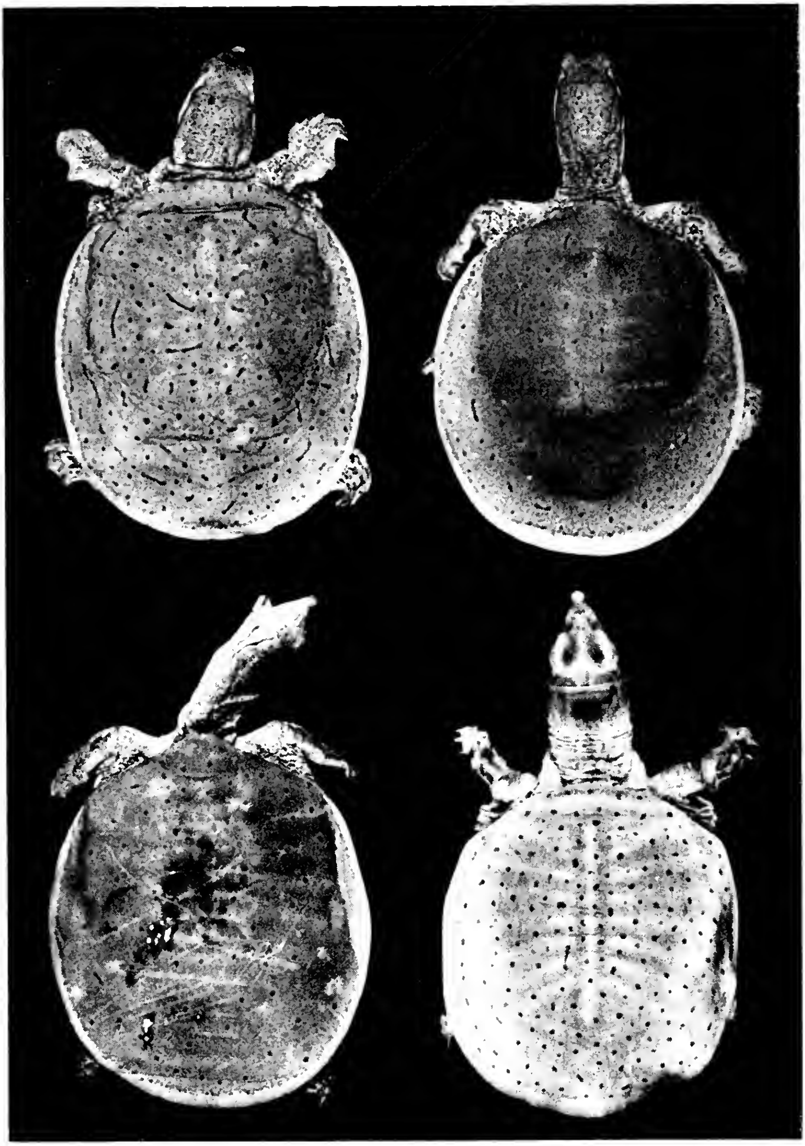
Trionyx spinifer emoryi, dorsal views. *Top*—Juveniles; left, UMMZ 69411 (× ¾), Rio Conchos, 9 mi. N Linares, Nuevo León, México; right, UMMZ 69412 (× ⅚), Río Purificación, north Ciudad Victoria, Tamaulipas, México. *Bottom*—Adult males; left, topotype, TU 11561 (× ⅓), Brownsville, Cameron County, Texas; right, KU 48217 (× ⅓), Black River Village, Eddy County, New Mexico.

PLATE 44



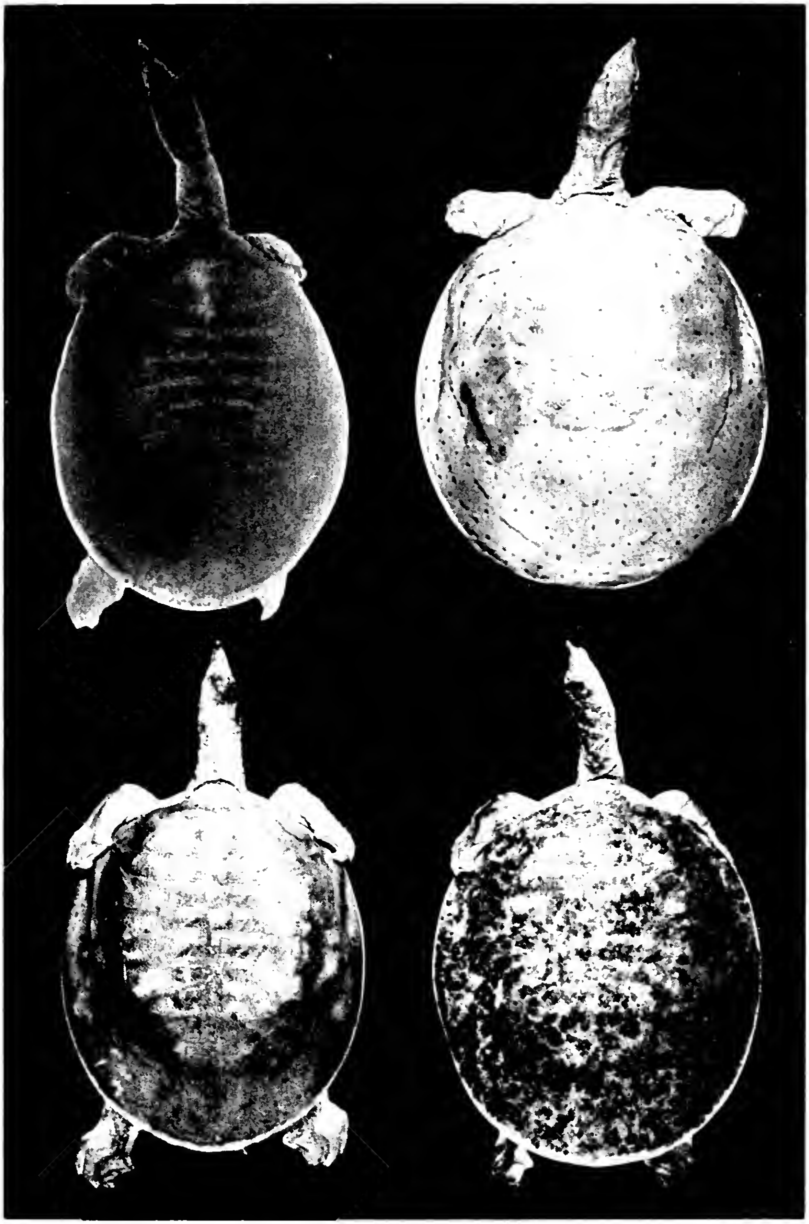
Trionyx spinifer emoryi, dorsal views. *Top*—Left, adult male, KU 51194 ($\times \frac{2}{7}$), Río Conchos, near Meoquí, Chihuahua, México; right, female, KU 3119 ($\times \frac{4}{9}$), Salt River, Phoenix, Maricopa County, Arizona. *Bottom*—Females; left, KU 3118 ($\times \frac{1}{5}$), locality same as KU 3119; right, TU 14453 ($\times \frac{3}{10}$), Pecos River, near junction with Independence Creek, Terrell County, Texas.

PLATE 45



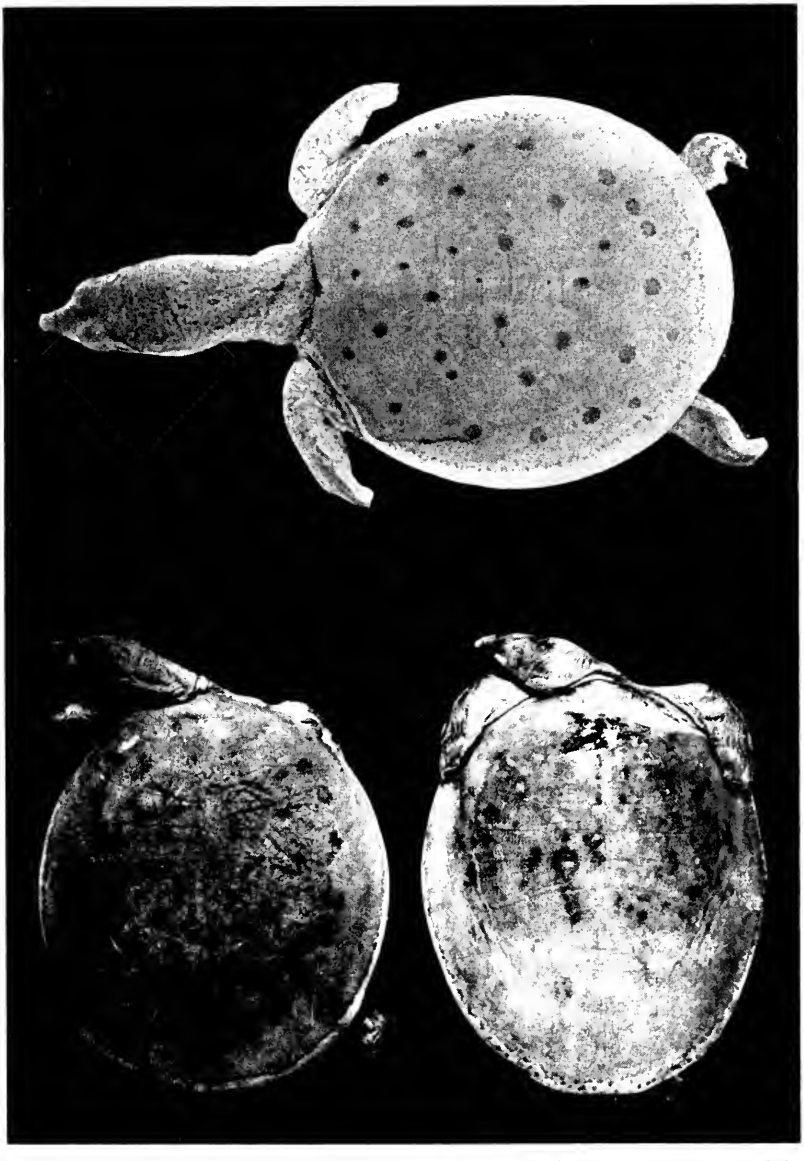
Trionyx muticus muticus, juveniles, dorsal views. *Top*—Topotypes (× 1), Wabash River, 2 mi. S New Harmony, Posey County, Indiana; left, INHS 7278; right, INHS 7279. *Bottom*—Left, TU 14375 (× ¾), Trinity River near junction with Big Creek, Liberty County, Texas; right, KU 50845 (× 1⅖), 4 mi. N Atwood, Hughes County, Oklahoma.

PLATE 46



Trionyx muticus muticus, dorsal views. *Top*—Adult males; left, TU 14606 ($\times \frac{3}{10}$), White River, Cotter, Marion County, Arkansas; right, KU 48237 ($\times \frac{1}{3}$), 8 mi. S Hanover, Washington County, Kansas. *Bottom*—Females ($\times \frac{1}{4}$), 2 mi. E Manhattan, in Pottawatomie County, Kansas; left, KU 48229; right, KU 48238.

PLATE 47



Trionyx muticus calvatus, dorsal views. *Top*—Juvenile, TU 17303 (× 1 2/5), Pearl River, Varnado, Washington Parish, Louisiana. *Bottom*—Left, adult male, KU 47118 (× 3/10), Pearl River within 4 mi. of Monticello, Lawrence County, Mississippi; right, adult female, TU 17306 (× 2/9), Pearl River, 9 mi. S Monticello, Lawrence County, Mississippi.

PLATE 48

FIG. 1. Habitat of *T. s. pallidus*, Little River, 6.5 mi. S Broken Bow, McCurtain County, Oklahoma, September 7, 1953.

FIG. 2. Habitat of *T. s. emoryi*, Río Mesquites, 2 mi. W Nadadores, Coahuila, México, July 27, 1959. Two *emoryi* were trapped in hoop nets set in quiet water to left of what is believed to be a muskrat house.

FIG. 1. General habitat of *T. s. pallidus* and *T. m. muticus*, Lake Texoma, in a period of low water, 2 mi. E Willis, Marshall County, Oklahoma, February 24, 1951.

FIG. 2. Type locality of *T. ater*, Tío Candido, 16 km. S Cuatro Ciénegas, Coahuila, México, July 30, 1959. An adult male of *T. s. emoryi* was also netted here.

Fig. 1. General habitat of *T. s. asper* and *T. m. calvatus*, Escambia River, 2 mi. E, ½ mi. N Century, Escambia County, Florida, June 1, 1954. Three nests of *calvatus* found on sand bar in foreground.

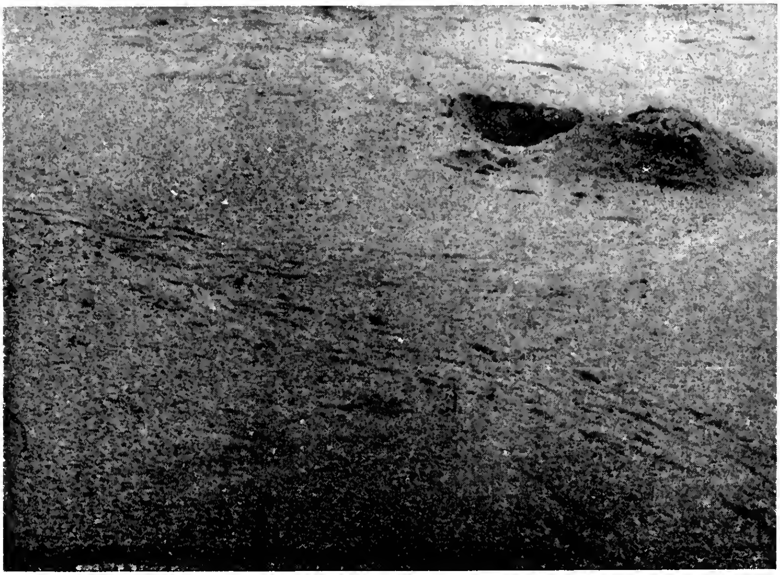


Fig. 2. Nest site of *T. m. calvatus* (excavated by investigator) on open sand bar shown above in Fig. 1, June 1, 1954. Note tracks of turtle in foreground leading toward and away from disturbed area at left.

PLATE 51

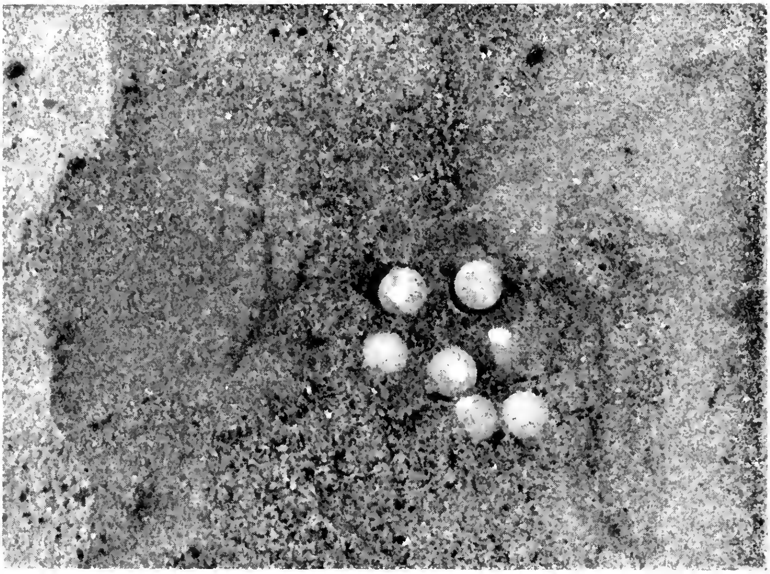


FIG. 1. Eggs of *T. m. calvatus in situ*, June 1, 1954, approximately six inches below surface, from nest shown in Fig. 2, Pl. 50. Note sandy substrate and seemingly irregular arrangement of eggs.

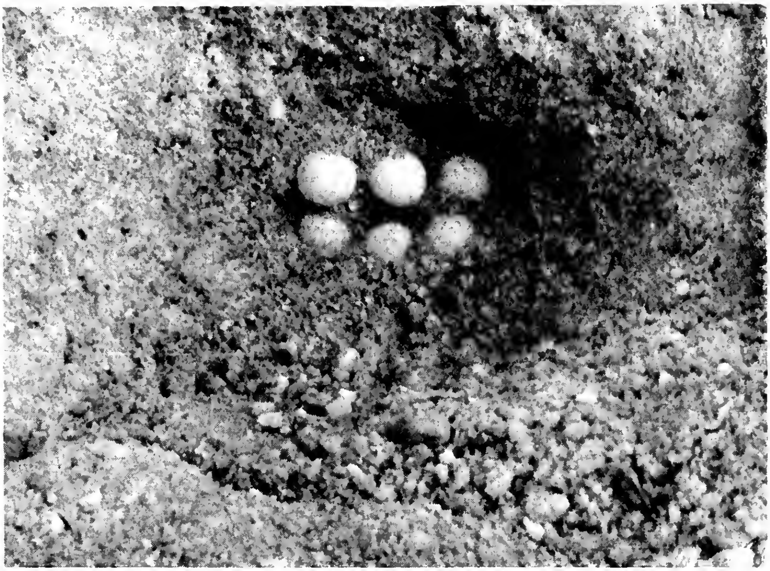
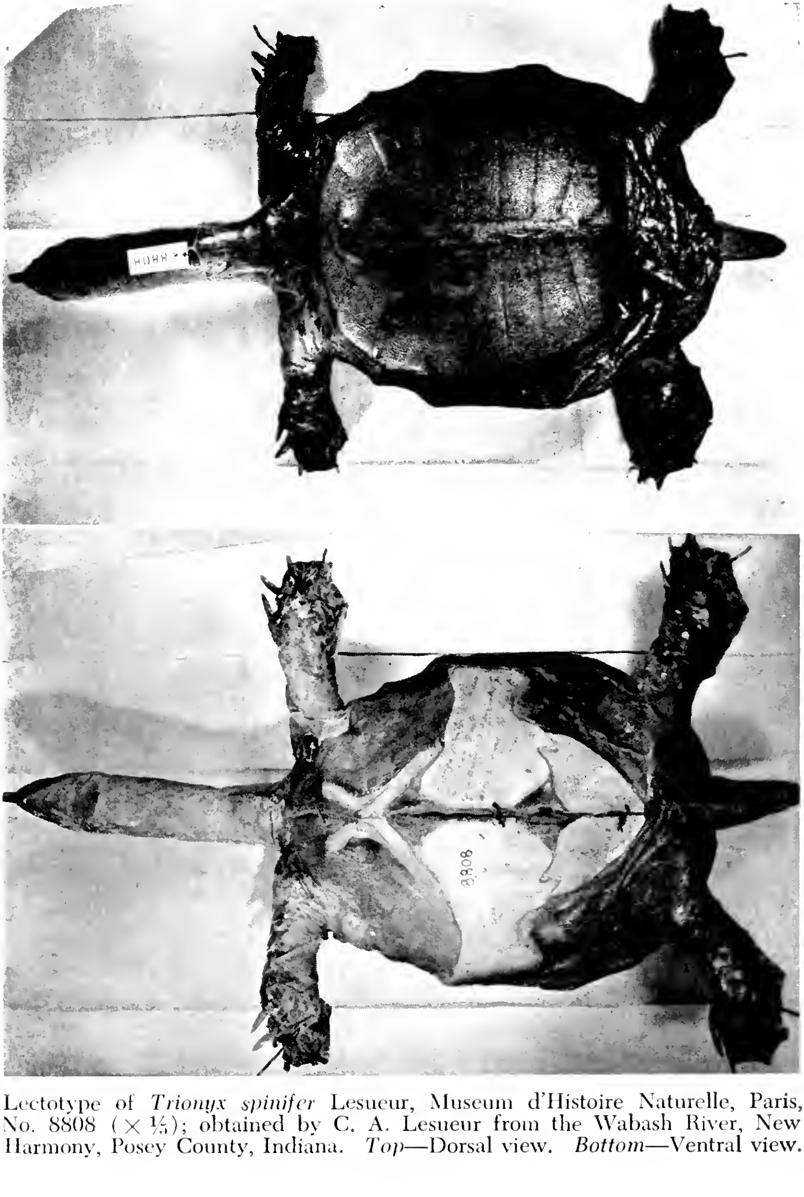


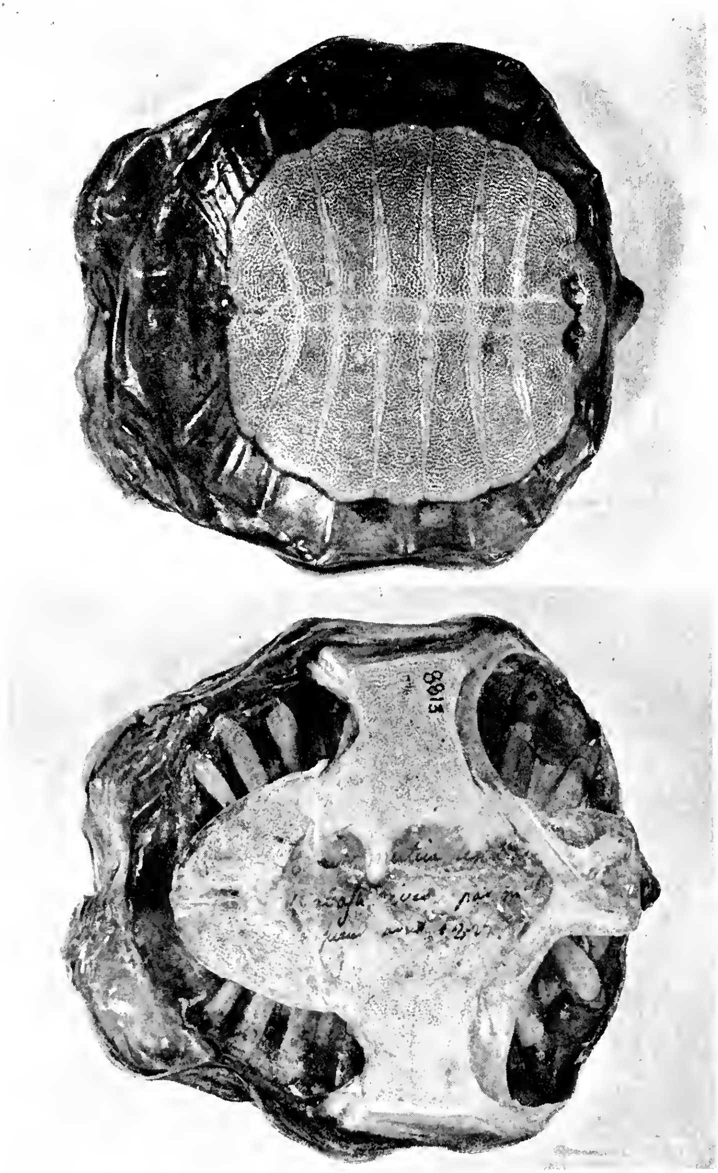
FIG. 2. Eggs of *T. m. calvatus in situ,* June 1, 1954; nest located at brim of incline shown in foreground of Fig. 1, Pl. 50. Note gravelly substrate (in foreground) and symmetrical arrangement of eggs.

PLATE 52



Lectotype of *Trionyx spinifer* Lesueur, Museum d'Histoire Naturelle, Paris, No. 8808 (× 1/5); obtained by C. A. Lesueur from the Wabash River, New Harmony, Posey County, Indiana. *Top*—Dorsal view. *Bottom*—Ventral view.

PLATE 53



Lectotype of *Trionyx muticus* Lesueur, Museum d'Histoire Naturelle, Paris, No. 8813 (× ½); obtained by C. A. Lesueur from the Wabash River, New Harmony, Posey County, Indiana. *Top*—Dorsal view. *Bottom*—Ventral view.

PLATE 54

Skull of holotype of *Platypeltis agassizi* Baur (= *T. s. asper*), MCZ 37172 (× 1), Savannah River, Georgia. *Top*—Dorsal view. *Bottom*—Ventral view.

INDEX TO VOLUME 13

New systematic names are in **boldface** type

—Univ. Kansas Publs. Mus. Nat. Hist., Vol. 13, 1960-1962.

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(Continued from inside of front cover)

Vol. 9.

1. Speciation of the wandering shrew. By James S. Findley. Pp. 1-68, 18 figures in text. December 10, 1955.
2. Additional records and extension of ranges of mammals from Utah. By Stephen D. Durrant, M. Raymond Lee, and Richard M. Hansen. Pp. 69-80. December 10, 1955.
3. A new long-eared myotis (Myotis evotis) from northeastern Mexico. By Rollin H. Baker and Howard J. Stains. Pp. 81-84. December 10, 1955.
4. Subspeciation in the meadow mouse, Microtus pennsylvanicus, in Wyoming. By Sydney Anderson. Pp. 85-104, 2 figures in text. May 10, 1956.
5. The condylarth genus Ellipsodon. By Robert W. Wilson. Pp. 105-116, 6 figures in text. May 19, 1956.
6. Additional remains of the multituberculate genus Eucosmodon. By Robert W. Wilson. Pp. 117-123. 10 figures in text. May 19, 1956.
7. Mammals of Coahuila, Mexico. By Rollin H. Baker. Pp. 125-335, 75 figures in text. June 15, 1956.
8. Comments on the taxonomic status of Apodemus peninsulae, with description of a new subspecies from North China. By J. Knox Jones, Jr. Pp. 337-346, 1 figure in text, 1 table. August 15, 1956.
9. Extension of known ranges of Mexican bats. By Sydney Anderson. Pp. 347-351. August 15, 1956.
10. A new bat (Genus Leptonycteris) from Coahuila. By Howard J. Stains. Pp. 353-356. January 21, 1957.
11. A new species of pocket gopher (Genus Pappogeomys) from Jalisco, Mexico. By Robert J. Russell. Pp. 357-361. January 21, 1957.
12. Geographic variation in the pocket gopher, Thomomys bottae, in Colorado. By Phillip M. Youngman. Pp. 363-387, 7 figures in text. February 21, 1958.
13. New bog lemming (genus Synaptomys) from Nebraska. By J. Knox Jones, Jr. Pp. 385-388. May 12, 1958.
14. Pleistocene bats from San Josecito Cave, Nuevo León, México. By J. Knox Jones, Jr. Pp. 389-396. December 19, 1958.
15. New subspecies of the rodent Baiomys from Central America. By Robert L. Packard. Pp. 397-404. December 19, 1958.
16. Mammals of the Grand Mesa, Colorado. By Sydney Anderson. Pp. 405-414, 1 figure in text, May 20, 1959.
17. Distribution, variation, and relationships of the montane vole, Microtus montanus. By Sydney Anderson. Pp. 415-511, 12 figures in text, 2 tables. August 1, 1959.
18. Conspecificity of two pocket mice, Perognathus goldmani and P. artus. By E. Raymond Hall and Marilyn Bailey Ogilvie. Pp. 513-518, 1 map. January 14, 1960.
19. Records of harvest mice, Reithrodontomys, from Central America, with description of a new subspecies from Nicaragua. By Sydney Anderson and J. Knox Jones, Jr. Pp. 519-529. January 14, 1960.
20. Small carnivores from San Josecito Cave (Pleistocene), Nuevo León, México. By E. Raymond Hall. Pp. 531-538, 1 figure in text. January 14, 1960.
21. Pleistocene pocket gophers from San Josecito Cave, Nuevo León, México. By Robert J. Russell. Pp. 539-548, 1 figure in text. January 14, 1960.
22. Review of the insectivores of Korea. By J. Knox Jones, Jr., and David H. Johnson. Pp. 549-578. February 23, 1960.
23. Speciation and evolution of the pygmy mice, genus Baiomys. By Robert L. Packard. Pp. 579-670, 4 plates, 12 figures in text. June 16, 1960.

Index. Pp. 671-690.

Vol. 10.

1. Studies of birds killed in nocturnal migration. By Harrison B. Tordoff and Robert M. Mengel. Pp. 1-44, 6 figures in text, 2 tables. September 12, 1956.
2. Comparative breeding behavior of Ammospiza caudacuta and A. maritima. By Glen E. Woolfenden. Pp. 45-75, 6 plates, 1 figure. December 20, 1956.
3. The forest habitat of the University of Kansas Natural History Reservation. By Henry S. Fitch and Ronald R. McGregor. Pp. 77-127, 2 plates, 7 figures in text, 4 tables. December 31, 1956.
4. Aspects of reproduction and development in the prairie vole (Microtus ochrogaster). By Henry S. Fitch. Pp. 129-161, 8 figures in text, 4 tables. December 19, 1957.
5. Birds found on the Arctic slope of northern Alaska. By James W. Bee. Pp. 163-211, plates 9-10, 1 figure in text. March 12, 1958.
6. The wood rats of Colorado: distribution and ecology. By Robert B. Finley, Jr. Pp. 213-552, 34 plates, 8 figures in text, 35 tables. November 7, 1958.
7. Home ranges and movements of the eastern cottontail in Kansas. By Donald W. Janes. Pp. 553-572, 4 plates, 3 figures in text. May 4, 1959.
8. Natural history of the salamander, Aneides hardyi. By Richard F. Johnston and Gerhard A. Schad. Pp. 573-585. October 8, 1959.
9. A new subspecies of lizard, Cnemidophorus sacki, from Michoacán, México. By William E. Duellman. Pp. 587-598, 2 figures in text. May 2, 1960.
10. A taxonomic study of the Middle American Snake, Pituophis deppei. By William E. Duellman. Pp. 599-610, 1 plate, 1 figure in text. May 2, 1960.

Index. Pp. 611-626.

(Continued on outside of back cover)

(Continued from inside of back cover)

Vol. 11. 1. The systematic status of the colubrid snake, Leptodeira discolor Günther. By William E. Duellman. Pp. 1-9, 4 figures. July 14, 1958.
2. Natural history of the six-lined racerunner, Cnemidophorus sexlineatus. By Henry S. Fitch. Pp. 11-62, 9 figures, 9 tables. September 19, 1958.
3. Home ranges, territories, and seasonal movements of vertebrates of the Natural History Reservation. By Henry S. Fitch. Pp. 63-326, 6 plates, 24 figures in text, 3 tables. December 12, 1958.
4. A new snake of the genus Geophis from Chihuahua, Mexico. By John M. Legler. Pp. 327-334, 2 figures in text. January 28, 1959.
5. A new tortoise, genus Gopherus, from north-central Mexico. By John M. Legler. Pp. 335-343. April 24, 1959.
6. Fishes of Chautauqua, Cowley and Elk counties, Kansas. By Artie L. Metcalf. Pp. 345-400, 2 plates, 2 figures in text, 10 tables. May 6, 1959.
7. Fishes of the Big Blue river basin, Kansas. By W. L. Minckley. Pp. 401-442, 2 plates, 4 figures in text, 5 tables. May 8, 1959.
8. Birds from Coahuila, México. By Emil K. Urban. Pp. 443-516. August 1, 1959.
9. Description of a new softshell turtle from the southeastern United States. By Robert G. Webb. Pp. 517-525, 2 plates, 1 figure in text. August 14, 1959.
10. Natural history of the ornate box turtle, Terrapene ornata ornata Agassiz. By John M. Legler. Pp. 527-669, 16 pls., 29 figures in text. March 7, 1960.
Index Pp. 671-703.

Vol. 12. 1. Functional morphology of three bats: Eumops, Myotis, Macrotus. By Terry A. Vaughan. Pp. 1-153, 4 plates, 24 figures in text. July 8, 1959.
2. The ancestry of modern Amphibia: a review of the evidence. By Theodore H. Eaton, Jr. Pp. 155-180, 10 figures in text. July 10, 1959.
3. The baculum in microtine rodents. By Sydney Anderson. Pp. 181-216, 49 figures in text. February 19, 1960.
4. A new order of fishlike Amphibia from the Pennsylvanian of Kansas. By Theodore H. Eaton, Jr., and Peggy Lou Stewart. Pp. 217-240, 12 figures in text. May 2, 1960.

More numbers will appear in volume 12.

Vol. 13. 1. Five natural hybrid combinations in minnows (Cyprinidae). By Frank B. Cross and W. L. Minckley. Pp. 1-18. June 1, 1960.
2. A distributional study of the amphibians of the Isthmus of Tehuantepec, México. By William E. Duellman. Pp. 19-72, pls. 1-8, 3 figures in text. August 16, 1960.
3. A new subspecies of the slider turtle (Pseudemys scripta) from Coahuila, México. By John M. Legler. Pp. 73-84, pls. 9-12, 3 figures in text. August 16, 1960.
4. Autecology of the copperhead. By Henry S. Fitch. Pp. 85-288, pls. 13-20, 26 figures in text. November 30, 1960.
5. Occurrence of the garter snake, Thamnophis sirtalis, in the great plains and Rocky mountains. By Henry S. Fitch and T. Paul Maslin. Pp. 289-308, 4 figures in text. February 10, 1961.
6. Fishes of the Wakarusa river in Kansas. By James E. Deacon and Artie L. Metcalf. Pp. 309-322, 1 figure in text. February 10, 1961.
7. Geographic variation in the North American Cyprinid fish, Hybopsis gracilis. By Leonard J. Olund and Frank B. Cross. Pp. 323-348, pls. 21-24, 2 figures in text. February 10, 1961.
8. Descriptions of two species of frogs, genus Ptychohyla; studies of American Hylid frogs, V. By William E. Duellman. Pp. 349-357, pl. 25, 2 figures in text. April 27, 1961.
9. Fish populations, following a drought, in the Neosho and Marais des Cygnes rivers of Kansas. By James Everett Deacon. Pp. 359-427, pls. 26-30, 3 figures in text. August 11, 1961.
10. North American recent soft-shelled turtles (family Trionychidae). By Robert G. Webb. Pp. 429-611, pls. 31-54, 24 figures in text. February 16, 1962.

Vol. 14. 1. Neotropical bats from western México. By Sydney Anderson. Pp. 1-8. October 24, 1960.
2. Geographic variation in the harvest mouse, Reithrodontomys megalotis, on the central great plains and in adjacent regions. By J. Knox Jones, Jr., and B. Mursaloglu. Pp. 9-27, 1 figure in text. July 24, 1961.
3. Mammals of Mesa Verde national park, Colorado. By Sydney Anderson. Pp. 29-67, pls. 1 and 2, 3 figures in text. July 24, 1961.
4. A new subspecies of the black myotis (bat) from eastern México. By E. Raymond Hall and Ticul Alvarez. Pp. 69-72, 1 fig. in text. December 29, 1961.
5. North American yellow bats, "Dasypterus," and a list of the named kinds of the genus Lasiurus Gray. By E. Raymond Hall and J. Knox Jones, Jr. Pp. 73-98, 4 figs. in text. December 29, 1961.
6. Natural history of the brush mouse (Peromyscus boylii) in Kansas with description of a new subspecies. By Charles A. Long. Pp. 99-110, 1 fig. in text. December 29, 1961.
7. Taxonomic status of some mice of the Peromyscus boylii group in eastern México, with description of a new subspecies. By Ticul Alvarez. Pp. 111-120, 1 fig. in text. December 29, 1961.

More numbers will appear in volume 14.

Vol. 15. 1. The amphibians and reptiles of Michoacán, México. By William E. Duellman. Pp. 1-148, pls. 1-6, 11 figures in text. December 20, 1961.
2. Some reptiles and amphibians from Korea. By Robert G. Webb, J. Knox Jones, Jr., and George W. Byers. Pp. 149-173. January 31, 1962.

More numbers will appear in volume 15.