Aug. 15, 1945

ZOOLOGY.—The subspecies and intergrades of the Florida burrowing crayfish, Procambarus rogersi (Hobbs).¹ HORTON H. HOBBS, Jr., University of Florida. (Communicated by WALDO L. SCHMITT.)

The first record of the presence of burrowing crayfishes occurring in the State of Florida that has come to my attention was that of Roland M. Harper (1914, p. 248). In discussing the Apalachicola flatwoods he states, "Much of the soil is too damp for ants, gophers, and salamanders, but crawfish are common in some places, if one may judge from their 'chimneys,' which are usually closed at the top, instead of open like the more familiar ones in more clayey soils farther inland." These burrows were probably constructed by one or more of the following crayfishes: P. rogersi campestris, P. rogersi ochlocknensis, P. rogersi intergrades, P. kilbyi,² P. apalachicolae,³ and P. latipleurum,⁴ all of which have been found in portions of the Apalachicola flatwoods.

The subspecies of Procambarus rogersi-P. r. rogersi, P. r. campestris, and P. r. ochlocknensis-are characterized by the structure of the first pleopod of the first form male. The mesial process is well developed, spiniform, or slightly compressed; the cephalic process is either lacking or is present as a reduced spine on the cephalodistal surface; the caudal process is large and thumblike, bent mesiad at a 15°-90° angle with the main shaft; the central projection is large and platelike, directed across the cephalodistal surface or obliquely distad in a cephalomesial to caudolateral direction. Hooks are present on the ischiopodites of only the third pereiopods of the male.

The subspecies are distinct, though forming at times unmistakable intergrades. Their ranges cover a considerable area in the eastern and central parts of the panhandle of Florida. The extreme eastern and western limits of the ranges of this assemblage are almost 100 miles apart, while the most northern and southern limits are separated by a distance of about 50 miles. Within these limits are portions of Bay, Gadsden, Gulf, Calhoun, Franklin, Leon, Liberty, and Wakulla Counties.

¹ Contribution from Department of Biology, University of Florida. Received February 27, 1945. ² Hobbs, 1940, p. 410. ³ Hobbs, 1942b, p. 55.

⁴ Hobbs, 1942b, p. 52.

All three are primary burrowers,⁵ with presumably poor powers of dispersal. Their ranges extend through a monotonous flatwoods, broken only here and there by small, scattered areas unsuitable for habitation by them. If rogersi had a higher vagility, such a range would seem to favor maintenance of a homogeneous population over the entire area, but instead the region is inhabited by small, local, inbred populations. When specimens from several of these are compared, it becomes evident that the subspecies of *P. rogersi* and their intergrades form a very heterogeneous complex.

The zone of intergradation consists of a large area in Franklin, Gulf, and Bay Counties and the southern parts of Liberty and Wakulla Counties. Toward the eastern side of this area, in eastern Franklin and western Wakulla Counties, specimens show a definite approach to rogersi campestris, which occurs in Leon and Wakulla Counties; west of the Apalachicola River, in northern Gulf County, material is closer to rogersi rogersi; while in the southern part of Liberty County the intermediates in most characters more closely resemble rogersi ochlocknensis. In general, the nearer one approaches the ranges of each of the three well-defined subspecies, the more nearly do the intermediates resemble typical material of the subspecies from that particular part of the range. The actual situation in respect to the intergrades is more complex than is here indicated and will be discussed more in detail following the descriptions of the subspecies.

SYSTEMATIC DISCUSSION

KEYS TO THE SUBSPECIES OF PROCAMBARUS ROGERSI⁶

Males

1. Caudal process of first pleopod bent but not so much as at a right angle to the main shaft of the appendage.....2

⁵ Primary burrowers are those crayfish that spend practically their entire lives in their burrows

⁶ It is not possible to construct a key to the intergrades of the several subspecies of *P. rogersi*. These are fully discussed on page 257.

Caudal process of first pleopod bent at a right angle to the main shaft of the appendage...

- - distal surface.....rogersi ochlocknensis

Females

- 1. Annulus ventralis only slightly if at all broader than long, usually longer than broad; cephalic margin cleft, with strongly developed tubercles......2 Annulus ventralis much broader than long; cephalic margin entire, with or without very low, rounded tubercles.....rogersi rogersi
- 2. Annulus ventralis subcylindrical; caudal half not anywhere flattened; cephalic half troughlike.....rogersi campestris
 - Annulus ventralis much longer than broad; caudal half flattened below with a single large, median, dome-shaped structure; cephalic half vatlike.....rogersi ochlocknensis

Procambarus rogersi rogersi (Hobbs)

Figs. 2, 14, 17, 22, 25

Cambarus rogersi Hobbs, 1938, pp. 61-65, figs. 1-11; 1940, p. 410.

Procambarus rogersi Hobbs, 1942a, p. 344.

Procambarus rogersi rogersi Hobbs, 1942b, p. 89, pl. 5, figs. 71-75, map 5.

Diagnosis.—Hooks present on ischiopodites of third pereiopods only; rostrum without lateral spines, areola obliterated in middle, or almost obliterated with a single row of punctations along fusion line of branchiostegites. First pleopod of first form male with platelike central projection directed across cephalic surface, caudal process noncorneous, thumblike, and bent caudomesiad at a right angle to the main shaft. Annulus ventralis broader than long; cephalic margin entire.

Description.—PARATYPIC MALE, FORM I: Carapace subovate. Width of carapace in region of caudodorsal margin of cervical groove greater than height (1.32–1.27 cm). Greatest width of carapace about midway between cervical groove and caudal margin of cephalothorax (1.45 cm).

Areola obliterated in middle, depressed, more than half as long as cephalic section of carapace (1.17-1.69 cm).

Rostrum broad-lanceolate; apex not reaching distal end of second joint of antennule peduncle; upper surface excavate, with a row of punctations along raised margins; margins gradually tapering to apex; no lateral spines present. Apex of rostrum directed ventrad, extreme apex abruptly bent upward. Subrostral ridges evident in dorsal view for over half the distance between postorbital ridges and tip of rostrum. Rostral ridges extending forward to apex of rostrum. Postorbital ridges extending caudad more than half the distance between apex of rostrum and cervical groove.

Surface of carapace punctate dorsad; granulate laterad. No lateral spines present. Suborbital angle lacking. Branchiostegal spines small.

Abdomen shorter and narrower than carapace. Anterior section of telson with one spine in the right and two in the left posterolateral angles.

Epistome broadly sublanceolate with slightly undulant margins; terminating cephalad in a small cephalomedian tubercle.

Antennules of the usual form; no spines present on ventral side of basal segment.

Antennae hardly reaching caudal margin of carapace when bent caudad. Antennal scale small; extending almost to end of second joint of peduncle of antennule. Spine on outer margin strong.

First pereiopod very broad and flattened, triangulate, with sharp apex. Inner margin of palm with a cristiform row of eight tubercles. Both surfaces of hand as well as fingers with setiferous punctations. Both fingers with two distinct ridges. Palm with a prominent ridge along articulation with movable finger. Movable finger: Dorsal surface with a prominent submedian ridge extending from base almost to tip. Outer margin studded with four tubercles along proximal third; remaining distal twothirds with about eight setiferous punctations. Opposable margin with excision slightly proximad of midlength; margin broken by two major tubercles (one at point of excision, the other near base of finger) between which are two smaller ones; four small tubercles present distad of distal major tubercle beyond which is a row of minute denticles extending almost to tip of finger. Immovable finger: Outer margin, in the form of a distinct ridge, with deep setiferous punctations; a few small tubercles present at base. Dorsal surface of finger with a prominent submedian ridge which curves inward at base following the general curvature of opposable margin of finger. Opposable margin interrupted by five tubercles, the second from base the largest. Carpus longer than broad; longer than inner margin of palm of chela; a deep longitudinal groove above; inner surface with three large tubercles and a few scattered smaller ones. Two large, acute tubercles on distal ventromesial surface. A single large, balllike tubercle on distal ventrolateral margin fits into a socket on lower surface of chela. *Merus* smooth except on lower surface which has an inner row of ten small, spikelike tubercles and an outer row of nine rounded ones.

Ischiopodite of third pereiopod hooked; hook strong, long.

First pleopod of male extending cephalad to base of second pereiopod. Tip terminating in three distinct parts. The mesial process, heavy but terminating in a spiniform tip, is bent caudolaterad. The cephalic process is absent. The caudal process is noncorneous, thumblike, and directed caudomesiad at a right angle to the main shaft of the appendage. The central projection is thin, corneous, and platelike and is directed across the cephalic surface of the appendage.

PARATYPIC MALE, FORM II: Differs from the male of the first form chiefly in the reduction of the sexual and secondary sexual characters, a total absence of corneous parts in the first pleopod, and a reduction of the hooks on the third pereiopods.

PARATYPIC FEMALE: Differs from the male of the first form in that the chelae are not so heavy, and there are slight variations in position and size of tubercles.

Annulus ventralis broader than long with fossa disappearing below left caudal margin. Cephalic margin entire with only very low rounded tubercles. A deep pit present in dextral half with rather steep walls except on cephalic and sinistral sides; caudal wall definitely overhanging. Sinus cutting caudal wall slightly sinistrad of midlength.

Measurements.—PARATYPIC MALE: Carapace, height 1.32, width 1.45, length 2.86 cm; areola, linear, length 1.17 cm; rostrum, length 0.28, width 0.35 cm; abdomen, length 2.40 cm; right chela, length of inner margin of palm 0.66, width of palm 1.11, length of outer margin of hand 1.92, length of movable finger 1.36 cm. PARATYPIC FEMALE: Carapace, height 1.20, width 1.27, length 2.48 cm; areola linear, length 0.96 cm; rostrum, length 0.33, width 0.33 cm; abdomen, length 2.30 cm; right chela, length of inner margin of palm 0.51, width of palm 0.88, length of outer margin of hand 1.57, length of movable finger 1.07 cm.

Type locality.—"Low pine flat-woods four miles north of Blountstown on State Highway no. 6" (Hobbs, 1938, p. 65).

Distribution .- Calhoun County, Fla.

Procambarus rogersi rogersi is endemic to Florida, and its range seems to be confined to a relatively small area in the panhandle of the State west of the Apalachicola River. Here it occupies a small area of flatwoods running north and south in the eastern part of Calhoun (and probably Gulf) County. Although no records of rogersi rogersi have been established in Gulf County, there are records of what I interpret as intergrades, P. r. rogersi × campestris, in the broad expanse of coastal flatwoods in the southern part of the county.

The linear form of the range of this subspecies may be explained by the distribution of the available flatwoods and the presence of the Apalachicola River on the east and the elevated strip of loamy Norfolk sand that extends on the east side of the River from Liberty County to the northern part of Franklin County. The combination of the two latter features certainly prevents migration eastward. The northern and western boundaries of the range are determined by well-drained soils that appear to form an efficient barrier to migration. The western boundary extends as far southward as the central part of Gulf County, but the southern limit of the range cannot be definitely set since the intergradation zone (rogersi × campestris × ochlocknensis) probably occurs in Gulf County.

Variation.—Procambarus rogersi rogersi seems to show little variation. In most of the specimens there is no spine present on the ventral surface of the basal joint of the antennule; however, occasionally there is a spine on one or both antennules. The cephalic process of the first pleopod of the male is generally not even present as a vestige, though occasionally it is strongly developed. The areola is sometimes not quite obliterated in middle. The epistome varies in form from semicircular to subtriangular.

Ecology.—Procambarus rogersi rogersi is a primary burrowing species and has been collected only in the flatwoods region around Blountstown. A definite plant association composed of pitcherplants (Sarracenia drummondi, S. flava, and S. psittacina), sundews (Drosera), club moss (Lycopodium), wiregrass, and hatpins (Ericaulon) is characteristic of the flatwoods flora where this crayfish has been taken. Generally in a locality in which these plants were observed from the road, burrows of some member of the rogersi group were found to be present; only in a few instances have I found no crayfish burrows in a situation of this type. In many places the water table is only a few inches below the surface, in others as deep as 3 feet.

The crayfish burrows are numerous in the Blountstown region, and since the chimneys range from 4 to 8 inches in height they are easily observed. The soil is a mixture of sand and clay underlain by clay, and the pellets composing the chimneys retain their rounded shape. Most of the chimneys are somewhat carefully constructed.

P. rogersi constructs a very complex burrow, which often extends horizontally 4 or 5 feet. Usually there are several passages—some that end blindly and others that open to the outside through chimneys. Generally, as in the case of the *advena*⁷ burrows, there is a single spiral passage that goes below the average water table. In some places the water is reached in less than a foot; in others it is about 2 feet below the surface. In any case, I have never had to dig more than 3 feet to reach the bottom of the passage.

In digging out a specimen from its burrow it is best to locate the deep passage and stir the water in it vigorously; allow it to become still, and within a very short time the crayfish will usually come to the surface. Occasionally it is necessary to dig to the bottom, or in

⁷ LeConte, 1856, p. 402.

some instances to dig out the entire burrow. Although most of my specimens have been taken from the deepest passage of the burrow I have found some clinging to the roots of wiregrass or of some other plant in the roof of one of the horizontal passages.

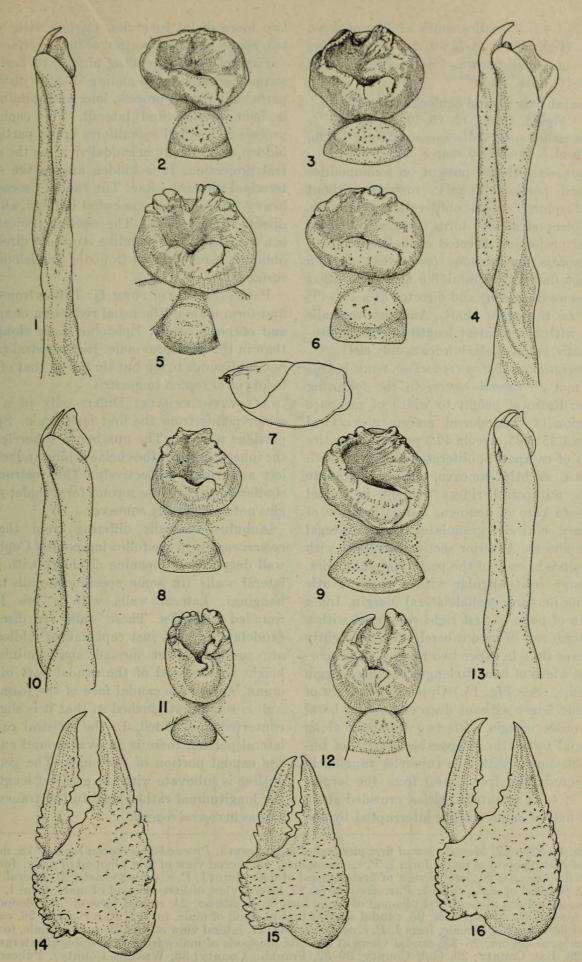
In one locality (about 8 miles north of Blountstown) the open, gently sloping flatwoods are essentially a large seepage area covering several acres. The ground is very spongy, and in spots, were it not for the heavy growth of grass, one would probably "bog down." In this locality the burrows are extremely numerous. As the water table is probably at the surface most of the year, the crayfish in their burrowing seem to expend their energy in constructing horizontal passages. In this locality the ground is so riddled with burrows that one can scarcely dig a spadeful of soil without exposing one of them.

In the burrows just mentioned an amphipod (Crangonyx sp.), an albinistic isopod (Asellus hobbsi Maloney), a beetle (Bidessus rogersi Young), and a copepod (Cyclops sp.) are abundant. On the crayfish were found some of the amphipods mentioned above, a branchiob-dellid [Cambarincola philadelphica (Leidy)], and an ostracod.

Although I have taken no other crayfish from burrows in the same habitat with *rogersi rogersi*, *P. kilbyi* was collected in large numbers from burrows and among the vegetation in a temporary stream close by.

Material examined.—CALHOUN COUNTY: 4 miles north of Blountstown [State Highway 6] (4-1335-1, 1σ I, $3 \circ \circ$), (4-1737-4, $2 \sigma \sigma$ I, $2 \sigma \sigma$ II, $1 \circ$); 8 miles north of Blountstown [State Highway 6] (4-1737-2, $5 \sigma \sigma$ I, $2 \sigma \sigma$ II, $3 \circ \circ$), (6-938-4, $2 \sigma \sigma$ II, $9 \circ \circ$); 9 miles north of Blountstown [State Highway 6] (4-738-11

FIGS. 1-16.—1, Caudal view of first pleopod of male, form II, Procambarus rogersi ochlocknensis; 2, annulus ventralis of P. r. rogersi from Calhoun County; 3, annulus ventralis of P. r. campestris from Leon County; 4, caudal view of first pleopod of male, form II, P. r. campestris; 5, annulus ventralis of an intergrade from Franklin County, west of the Apalachicola River; 6, annulus ventralis of an integrade from Franklin County, near the Franklin-Wakulla County line; 7, lateral view of carapace of P. r. campestris; 8, annulus ventralis of an intergrade from Franklin County 10 miles west of Carrab belle; 9, annulus ventralis of an intergrade from Franklin County 7 miles west of Carrabelle; 10, caudal view of first pleopod of male, form I, P. r. ochlocknensis from Liberty County; 11, annulus ventralis of P. r. ochlocknensis from Gadsden County; 12, annulus ventralis of P. r. ochlocknensis from Liberty County; 13, Caudal view of first pleopod of male, form I, P. r. ochlocknensis from Gadsden County; 14, upper surface of chela of P. r. rogersi from Calhoun County; 15, upper surface of chela of P. r. ochlocknensis from Liberty County; 16, upper surface of chela of P. r. campestris from Leon County. The drawings of the chelae (Figs. 14-16) were made from paratypes, and so there are some discrepancies in the illustrations and text in the number and distribution of tubercles. Pubescence has been removed from all structures figured.



FIGS. 1-16.—(See opposite page for legend.)

 $2 \sigma \sigma I$, 1φ); 2.5 miles south of Blountstown [State Highway 6] (4-738-9, $1 \sigma I$); 5.5 miles south of Blountstown [State Highway 6] (5-341-16, $1 \sigma I$, 1φ).

Procambarus rogersi ochlocknensis Hobbs Figs. 1, 10, 11, 13, 15, 19, 20, 26

Procambarus rogersi ochlocknensis Hobbs, 1942b, p. 89, pl. 5, figs. 76-80, map 5.

Diagnosis.—Hooks present on ischiopodites of third pereiopods only; rostrum without lateral spines; areola obliterated in middle. First pleopod of first form male with fanlike central projection directed caudolaterad; caudal process noncorneous (somewhat swollen but not distinctly thumblike as in the other subspecies of rogersi) and directed at a $15^{\circ}-40^{\circ}$ angle to the main shaft. Annulus ventralis ovate with the greatest length in the longitudinal axis, the cephalic border deeply cleft.

Description.-HOLOTYPIC MALE, FORM I: Differs from P. rogersi rogersi in the following points: Ratio of height to width of carapace in region of caudodorsal margin of cervical groove 1.25:1.23. Areola 42.3 per cent of entire length of carapace; obliterated. Rostrum with margins slightly concave, deeply excavate above. Subrostral ridges evident in dorsal aspect to base of acumen. Lateral surface of carapace entirely granulate. Branchiostegal spines absent. Anterior section of telson with two spines in each of the posterolateral angles. Epistome subtriangular with a single gentle swelling on each cephalolateral margin. Inner margin of palm of first right pereiopod with a cristiform row of nine tubercles. Chela slightly narrower than in other two races (i.e., proportion of width of hand to length of inner margin of palm). (See Fig. 15.) Opposable margin of movable finger without deep excision in basal half; outer margin with two tubercles along proximal two-fifths. Opposable margin of immovable finger with five tubercles ranging in size (numbering from base) from the largest 3, 5, 2, 4, 1; minute denticles crowded along distal half of same margin interrupted by the two more distal tubercles. Carpus with only two spines on distal portion of inner surface.

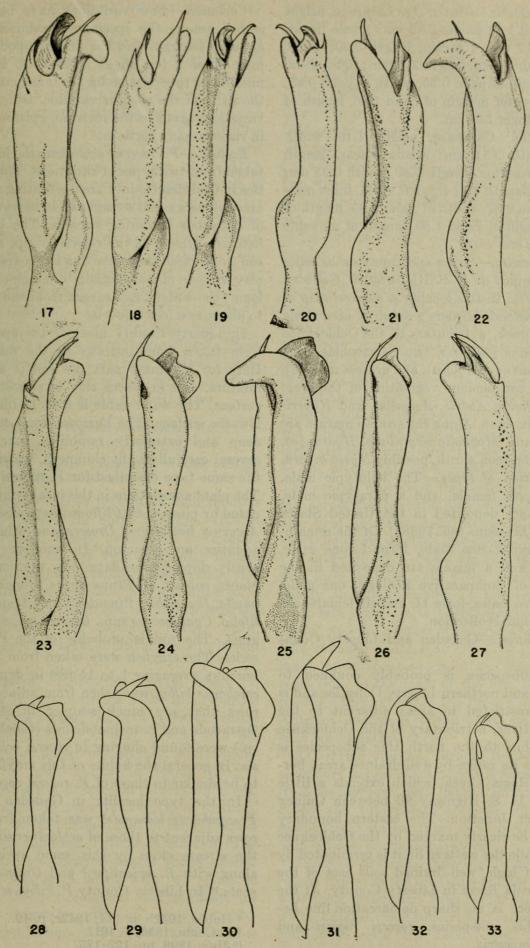
First pleopod extending almost to base of second pereiopod; tip ending in four distinct parts. The mesial process, long and spiniform, is bent caudad and laterad. The cephalic process is a small spiculiform spine partially hidden, particularly in caudal view, by the central projection. It is hidden among the subterminal plumose setae. The caudal process is heavy, noncorneous, somewhat inflated, and is directed mesiodistad. The central projection is a corneous, thin, platelike structure directed obliquely caudolaterad from the cephalodistal surface.

PARATYPIC MALE, FORM II: Differs from the first form male in the usual reduction of spiny and corneous parts. Epistome more elongate than in the first form male. Right rostral ridge not continuous to tip but similar to that of the holotype of *rogersi campestris*.

ALLOTYPIC FEMALE: Differs only in a few minor points from the first form male. Spiny portions reduced. The number of tubercles on the inner margin of the chelae is nine and seven, left and right, respectively. The rostrum is similar to that of the second form male; margins not as decidedly concave.

Annulus ventralis differing from that of rogersi rogersi in the following points: Cephalic wall deeply cleft; opening ditchlike with high lateral walls (in some specimens walls overhanging). Lateral walls with a few large rounded tubercles. These walls are directed caudolaterad, and just cephalad of midlength are suddenly bent mesiad and diminish in height to the level of the caudal part of the organ. Across the caudal face of the fossa the wall is somewhat pinched so that it is slightly contorted and folded. In the sinistral caudolateral portion there is an oval mound cut by the caudal portion of the sinus. The general outline is subovate with the greatest length in the longitudinal rather than in the transverse axis as in rogersi rogersi.

FIGS. 17-33.—17, Mesial view of first pleopod of male, form I, Procambarus rogersi rogersi; 18, mesial view of first pleopod of male, form I, P. r. campestris; 19, mesial view of first pleopod of male, form I, P. r. ochlocknensis; 20, lateral view of first pleopod of male, form I, P. r. campestris; 22, lateral view of first pleopod of male, form I, P. r. rogersi; 23, mesial view of first pleopod of male, form I, P. r. campestris; 22, lateral view of first pleopod of male, form I, P. r. rogersi; 23, mesial view of first pleopod of male, form I, P. r. campestris; 25, caudal view of first pleopod of male, form I, P. r. rogersi; 26, caudal view of first pleopod of male, form I, P. r. cochlocknensis; 27, lateral view of first pleopod of male, form I, P. r. rogersi; 26, caudal view of first pleopod of male, form I, P. r. ochlocknensis; 27, lateral view of first pleopod of male, form I, P. r. ochlocknensis; 27, lateral view of first pleopod of male, form I, P. r. ochlocknensis; 27, lateral view of first pleopod of male, form I, P. r. ochlocknensis; 27, lateral view of first pleopod of male, form I, P. r. ochlocknensis; 27, lateral view of first pleopod of male, form I, P. r. ochlocknensis; 27, lateral view of first pleopod of male, form I, P. r. ochlocknensis; 27, lateral view of first pleopod of male, form I, P. r. ochlocknensis; 27, lateral view of first pleopod of male, form I, P. r. ochlocknensis; 28–33, caudal views of the first pleopods of males from the region of intergradation (28, Bay County; 29, Gulf County; 30–32, Franklin County; 33, Wakulla County). Pubescence has been removed from all structures figured.



FIGS. 17-33.—(See opposite page for legend.)

Measurements.—HOLOTYPE: Carapace, height 1.25, width 1.23, length 2.65 cm; areola linear, length 1.12 cm; rostrum, length 0.30, width 0.35 cm; abdomen, length 2.37 cm; right chela, inner margin of palm 0.55, width of palm 0.88, length of outer margin of hand 1.56, length of movable finger 1.05 cm.

ALLOTYPE: Carapace, height 1.16, width 1.27, length 2.51 cm; areola linear, length 0.96 cm, rostrum, length 0.30, width 0.35 cm; abdomen, length 2.31 cm; left chela, inner margin of palm 0.57, width of palm 0.95, length of outer margin of hand 1.50, length of movable finger 1.00 cm.

Type locality.—Seven and three-tenths miles west of Quincy on U. S. Highway 90, Gadsden County, Fla. In this locality a narrow strip of grassy flatwoods borders a swampy area along Telogia Creek, a tributary to the Ochlocknee River. Pinus palustris, two Sarracenias (perhaps psittacina and flava), and grasses make up the more conspicuous vegetation of the area, while Pogonia, Aletris, Ascyrum, and Hypericum are common. Along the swamp margin are Cerothamnus, Magnolia virginiana, Hydrangea, and an evergreen shrub, possibly Nyssa biflora.

Disposition of types.—The holotypic male, the allotypic female, and a paratypic male, form II, are deposited in the United States National Museum (no. 79383). Of the remaining paratypes, one male, form I, one male, form II, and a female are deposited in the Museum of Comparative Zoology; one male, form I, five males, form II, and six females are in my personal collection.

Distribution.-Gadsden and Liberty Counties, Fla.

This subspecies is probably confined to Gadsden and northern Liberty Counties and is perhaps restricted to areas adjacent to the Telogia River, a tributary of the Ochlocknee River. Thus to the north this subspecies is limited in its range by well-drained areas bordering Telogia Creek, which extends a little north of U.S. Highway 90 between Quincy and River Junction. The eastern boundary seems to be clearly marked by the Ochlocknee River, while the western limit is terminated by a strip of high, well-drained soils east of the Apalachicola River in Liberty County. At the south there is no sharp demarcation line between this subspecies, rogersi rogersi and rogersi campestris.

Variation.—Few variations have been observed among the specimens examined. The annulus ventralis and the first pleopod of the male show a few slight differences, and the number of tubercles along the inner margin of the palm of the chela is variable. Other slight variations occur in the rostrum, epistome, and in various spiny portions.

Ecology.—P. rogersi ochlocknensis has been taken from two types of situations. The localities in Gadsden County are fluctuating seepage areas along a small stream and in narrow strips of flatwoods bordering streams. The burrows here are typical of the rogersi group, and the soil from which they were dug is a coarse sandy clay in some places overlain by muck or sandy loam; the water table ranges from the surface to about two feet below it.

In Liberty County most of the specimens were taken from burrows in the flatwoods. Here for the most part the soil is a sandy mixture, and in places clay is almost at the surface. The water table is 6 to 18 inches below the surface. The burrows are 1 to 2 feet deep and extremely rambling, many with several carefully built chimneys, which are of the same type described for P. rogersi rogersi. The plant associations in this locality are dominated by pines, ti-ti (Cliftonia monophylla), and Ascyrum linifolium; Drosera and other semiaquatics are common. In another area of gently sloping pine flatwoods, the commoner plants consist of Pinus sp., Cliftonia monophylla, Ilex glaber, Pinguicula sp., Aronia arbutifolia, Cyanococcus spp., Drosera sp., and wiregrass. The soil is probably of the Plummer series. The crayfish were taken from complex burrows averaging 1 to $1\frac{1}{2}$ feet in depth. Procambarus kilbyi was taken from adjacent burrows that are much simpler in structure. Ostracods and branchiobdellids (Cambarincola sp.) were found clinging to rogersi ochlocknensis. In general the habits of this crayfish seem to be similar to those of P. rogersi rogersi.

In the type locality in Gadsden County Procambarus leonensis⁸ was taken from burrows adjacent to those of ochlocknensis, and in the stream close by this same species was, along with P. spiculifer,⁹ and Orconectes clypeata.¹⁰ In Liberty County P. kilbyi was taken

⁸ Hobbs, 1942b, p. 114; 1942c, p. 49.

⁹ LeConte, 1856, p. 401.

¹⁰ Hay, 1899, pp. 122-123.

from burrows interspaced among the burrows of *ochlocknensis*.

Material examined.—GADSDEN COUNTY: 7.3 miles west of Quincy [U. S. Highway 90] (4-1437-1, 1 ♂I, 1 ♀), (3-1739-3, 1 ♀), (5-141-1a, 2♂♂I, 2♂♂II, 2♀♀); 8.3 miles southwest of junction of State Highways 12 and 135 on Highway 135 (5-141-3, 1 JI, 1 9); 2.7 miles southwest of junction of U.S. Highway 90 and State Highway 12 on Highway 12 (5-141-2, 1 JII). LIBERTY COUNTY: 4.5 miles north of Hosford [State Highway 135] (5-141-5, 3 J JII, $3 \circ \circ$). The remaining specimens from following localities are slightly atypical: Near Hosford (12-937-1a, 1 JI); 1.6 miles west of the Ochlocknee River [State Highway 19] (3-1639-1a, 1 ♂I, 1 ♂II, 8 9 9); 4 miles east of Hosford [State Highway 19] (3-1739-1a, 2 J JI, 2♂♂II, 7♀♀, 2♀♀ with eggs, 1♂ imm., 1 9 imm.); 9 miles west of Hosford [State Highway 19] (3-1739-8a, 1 9); near Hosford (8-234-1, 1 9); 3.5 miles east of Hosford [State Highway 19] (4-841-1, 23 3 II, 1 9 with eggs).

Procambarus rogersi campestris Hobbs

Figs. 3, 4, 7, 16, 18, 21, 24

Procambarus rogersi campestris Hobbs, 1942b, p. 90, pl. 6, figs. 81-85, map 5.

Diagnosis.—Hooks present on ischiopodites of third pereiopods only; rostrum without lateral spines; areola obliterated in middle. First pleopod of first form male with fanlike central projection directed across cephalic surface; caudal process thumblike and directed at a 45° angle to the main shaft. Annulus ventralis subcylindrical with cephalic border open; troughlike with high, multituberculate lateral ridges.

Description.—HOLOTYPIC MALE, FORM I: Differing from one or the other subspecies in the following points: Width of carapace greater than height (1.65:1.45 cm). Areola 40.9 per cent of entire length of carapace. Areola obliterated; no punctations in fusion line of branchiostegites. Subrostral ridges prominent; rostral ridges do not extend to tip of rostrum. (See Fig. 7.) Cephalic region in lateral aspect not evenly rounded. Lateral surfaces of carapace granulate. Branchiostegal spines absent. Anterior section of telson with two spines in each of the posterolateral angles. Epistome broadly subovate with an acute cephalomedian projection. Antennules with a spine present on ventral side of basal segments. Inner margin of palm of first pereiopod with a cristiform row of nine tubercles. Opposable margin of movable finger with deep excision in basal half. Outer margin with five tubercles on proximal half. Outer margin of immovable finger bearing a row of tubercles along proximal half and setiferous punctations on distal half. The one major tubercle on opposable margin lies somewhat distad of midway between the two major tubercles on movable finger. Two smaller tubercles proximad of the major tubercle. A single row of minute denticles along distal half is broken at intervals by five tubercles.

First pleopod extending to base of second pereiopod, distinctly separated at tip; tip ending in four parts. The mesial process is heavy and sinuate (in mesial view), tapering to a point; bent obliquely and laterally, passing beneath the caudal process. The cephalic process is much reduced (can be seen only in mesial and cephalic views), and is closely applied to the central projection at the base of the cephalomesial face. The caudal process is large and thumblike and extends at a 45° angle to the main shaft in a mesiodistal direction. The central projection forms a large corneous fan across the cephalic side of the tip and is also bent at about a 45° angle to the main shaft; however, directed laterodistad.

PARATYPIC MALE, FORM II: Differs from the first form male in only a few minor details, chiefly in the reduction of the sexual and secondary sexual parts (there being no corneous parts), and the number of tubercles and spines. The cephalic process of the first pleopod is much more conspicuous in the second form male than in the male of the first form. The rostral ridges extend to the tip of the acumen. Anterior section of telson with one spine in each posterolateral angle.

ALLOTYPIC FEMALE: Besides the sexual and secondary sexual characters, the female differs from the first form male in the following points: Spiny and tuberculate portions slightly different; right rostral ridge as in holotype; left as in second form male paratype.

Annulus ventralis differing from that of rogersi rogersi in the following points: Cephalic wall open, troughlike, with rather high lateral walls. Lateral walls tuberculate cephalad, and continuous with the caudal wall which is lower, decidedly lower left of the midventral line. Whereas the annulus of *rogersi rogersi* is subovate and broader than long, the annulus of *rogersi campestris* is subcylindrical.

Measurements.—HOLOTYPE: Carapace, height 1.45, width 1.65, length 3.15 cm; areola linear, length 1.29 cm; rostrum, length 0.40, width 0.39 cm; abdomen, length 2.90 cm; right chela, inner margin of palm 0.74, width of palm 1.28, length of outer margin of hand 2.19, length of movable finger 1.46 cm. ALLOTYPE: Carapace, height 1.35, width 1.54, length 3.02 cm; areola, linear, length 1.15 cm; rostrum, length 0.36, width 0.39 cm; abdomen, length 2.90 cm; right chela, inner margin of palm 0.65, width of palm 1.12, length of outer margin of hand 1.97, length of movable finger 1.34 cm.

Type locality.—A low, pine flatwoods about 12 miles south of Tallahassee, Leon County, Fla., along the east side of Horseshoe Bay (the exact location: Sec. 16–17, T. 25, R. 2 W.). This locality is a typical sour-gum and ti-ti bay region. The hammock is quite low, with very acid soil and water, and is subject to flooding in wet weather. The soil is largely muck and sand, and at the time of digging the water table was about 3 feet below the surface. Pines, wiregrass, palmetto, gallberry, and ti-ti shrubs are characteristic of the flora, and pitcherplants and sundews are common.

Disposition of types.—The holotypic male, form I, the allotypic female, and a form II male paratype are deposited in the United States National Museum (no. 79384). Two female paratypes are in the Museum of Comparative Zoology. The remaining paratypes, one male, form I, one male, form II, and 13 females are in my personal collection.

Distribution .- Leon and Wakulla Counties.

The typical forms of *P. rogersi campestris* are found in the southwestern part of Leon and northwestern part of Wakulla Counties. This subspecies is also a Florida endemic and probably occupies the greater portion of the western half of Wakulla and the southwestern quarter of Leon Counties.

The range of *campestris* is bounded on the west by the Ochlocknee River, which, together with the well-drained soils adjacent to it, serves as an effective barrier in Leon and the northern part of Wakulla Counties but is only a partial barrier in the southern part of Wakulla County; the eastern boundary is a region of high, well-drained soils extending through the middle of Wakulla County to the Gulf. The northern boundary lies in the southwestern part of Leon County where the flatwoods end in well-drained, rolling hills.

Variation.—There is no indication of inbred local populations among my specimens of *P. rogersi campestris;* the only differences observed seem to be individual ones, involving sizes and positions of spines and tubercles.

Ecology.—Like the other members of this species, rogersi campestris is a primary burrower, apparently confined to flatwoods. The flatwoods east of the Ochlocknee River are not markedly different from those described in the discussion of the ecology of *P. rogersi rogersi*, except that the soil is underlain by hardpan rather than clay. There are pines, wiregrass, pitcherplants, sundews, etc., and the soil is much the same general type—that is, most of it is poorly drained and supports an abundant growth of semiaquatic plants.

The burrows are very complex and often run horizontally for several feet; many of them reach the surface in several places. On one occasion I dug into one of these burrows and followed the spiral passage downward for 5 feet and still had not reached the bottom. This burrow was about a hundred yards from the border of a bayhead, and its unusual depth was probably explained by the fact that just prior to the time I collected here there had been an unusually long dry season.

Several specimens of Crangonyx sp. were taken from the burrows, some of them clinging to the abdomens of the crayfish. Many ostracods and branchiobdellid worms (*Cambarincola vitrea* Ellis) were found clinging to the crayfish.

In only two instances has another species been collected with *rogersi campestris*. *P. kilbyi* was taken from burrows adjacent to those of *campestris*. The burrows of the two species, however, are very distinct in that those of *kilbyi* are generally simple, while those of *campestris* are very complex.

Material examined.—LEON COUNTY: 12 miles southwest of Tallahassee (11-2736-1, 2 J J'I, 2 J J'II, 10 9 9). WAKULLA COUNTY¹¹: 28

¹¹ Perhaps some of the locality records from Wakulla County should be listed under the intergrade localities, although most of the specimens taken here are scarcely to be distinguished from typical *campestris*. miles north of Sopchoppy [State Highway 127] (6-538-6, $1 \triangleleft I$); 2 miles south of Sopchoppy [U. S. Highway 319] (5-2940-8, $1 \triangleleft II$, $4 \triangleleft \varphi$, $2 \triangleleft \varphi$ imm.); 7.5 miles northwest of Sopchoppy [State Highway 127] (6-538-8b, $1 \triangleleft$); 7 miles north of Sopchoppy [State Highway 127] (6-538-9, $1 \triangleleft II$); 16 miles southwest of Tallahassee (8-0436-2, $6 \triangleleft \varphi$).

INTERGRADES

The characters in which the evidences of intergradation are most clearly seen are the structure of the first pleopod of the male and of the annulus ventralis of the female. The variations in these structures are gradual and essentially quantitative rather than discontinuous ones. In the male there is, from one extremity of the range to the other, a gradual change in the degree of bending of certain of the terminal processes and in the relative sizes of the various tips. (See Figs. 1, 4, 10, 13, and 17-33.) For example, the caudal process of the first pleopod of the males from Calhoun County (rogersi) is bent laterad at a right angle to the main shaft of the appendage. In specimens from Gulf and Franklin Counties, west of the Apalachicola River (intergrades), the process, while bent, forms less than a right angle with the main shaft. Specimens from Franklin County east of the Apalachicola River and from southern Liberty County (intergrades) have this process even more erect, and finally, in material from Wakulla and Leon Counties (campestris), and from northern Liberty and Gadsden Counties (ochlocknensis), the process is still more nearly straight. In the region of intergradation occasional specimens occur which are structurally out of place, but considering the series as a whole the gradation is quite evident.

Similarly the annulus ventralis shows gradual changes in gross shape, in configuration of the fossa and sinus, and in surface contour. (See Figs. 2, 3, 5, 6, 8, 9, 11, and 12.) In specimens from Calhoun County (rogersi) this structure is subelliptical, with the longest axis directed laterad and with only a few very small tubercles on the cephalic border, which is entire. In specimens from west of the Apalachicola River in Bay and Gulf Counties (intergrades) the annulus is broader than long, but this characteristic is not so marked as in the Calhoun County females; the tubercles on the cephalic border are also more strongly developed. In specimens from east of the Apalachicola in Franklin and Liberty Counties (intergrades) the annulus ventralis is more elongate and the tubercles decidedly higher. The opposite extreme from the annulus ventralis of the Calhoun County specimens is seen in the females from Gadsden County(ochlocknensis). Here it is much longer than broad, the cephalic margins strongly tuberculate and cleft. The campestris population in Wakulla and Leon Counties has the annulus ventralis more like the Franklin County intergrades.

Additional similarly merging variations may be noted in the figures of these structures. While there are other differences between the three geographic races, they do not show so clearly the gradual blending exhibited by the first pleopod of the male and the annulus ventralis of the female.

As shown by the accompanying map, the area inhabited by the intergrades is larger than the combined ranges of the three defined races, and extends considerably to the west along the coast. That the population of this area does not itself constitute a recognizable race distinct from the others, as might be suspected on geographical grounds, becomes evident when the variation described above is further analyzed. In western Franklin County the crayfish are most nearly intermediate in characteristics between r. rogersi, r. campestris, and r. ochlocknensis, and at the same time are the most heterogeneous, showing the most variable admixtures of the characters of the three races. The farther east one goes in Franklin and southern Wakulla Counties the more nearly does the population approach campestris, while in northern Franklin and southern Liberty counties a similar approach occurs to typical ochlocknensis. Just west of the Apalachicola River the population is still highly variable, but shows a tendency toward rogersi, and probably intergrades fully with that race in the north-central part of Gulf County. Farther west the population is still heterogeneous, though closer to rogersi than to either of the more eastern races; however, it can not even be called atypical rogersi, since features suggesting campestris and ochlocknensis, which are never present in typical rogersi, occur in individual specimens.

Two rather startling situations involving

specimens from local areas in Bay County deserve further remarks. One of these peculiar situations arises in the peninsula, herein designated as the San Blas Peninsula, between East Bay and the Gulf. The first pleopods of the males taken in this peninsula are almost typical of rogersi rogersi from Calhoun County, while the annulus ventralis in the females is not nearly so typical-being similar to that of the intergrades found in other sections of Bay County and in Gulf County. This condition is peculiar, since both males and females from the mainland to the north and east are definitely of the intergrade types. Perhaps an explanation for this apparently local condition may be made by the further assumption that rogersi rogersi had already become differentiated by the end of the Pamlico submergence, and as the land emerged to the south, this species followed the retreating shore line, moving out into the area now constituting the San Blas Peninsula. Subsequent influx of the ochlocknensis and the campestris stocks from the east resulted in the intergradation (hybridization) of these stocks in Gulf and Bay counties, but at the same time establishing two semi-isolated areas of rogersi rogersi-one in Calhoun County, the range of typical rogersi, and the other in the San Blas Peninsula, the later perhaps being more subject to intergradation than the former because of its geographical and less well isolated position.

The other region that needs further remarks is the one seemingly isolated on the west side of West Bay. I have only three specimens from the West Bay region, a male, form I, taken 1.5 miles north of West Bay, and two females collected about 1 mile south of it. The pleopod of the male very closely approximates that of rogersi campestris, but the annuli ventralis, the rostra, and chelae are not typical of any of the subspecies. It has been supposed that there was a continuous area occupied by rogersi across the northern shore of both East and West Bay, but recently in attempting to collect this species in this area I drove north along State Highway 52 through the flatwoods section and west from Vicksburg to West Bay on State Highway 83 and was unable to locate a single rogersi burrow. This, of course, does not indicate the absence of rogersi in the area, but the fact that I did not find it there at least opens the question as to what path of migration the stock

took to reach the western shore of West Bay. This might lead one to wonder whether or not the San Blas Peninsula and the adjacent peninsula to the west were at one time connected.

The coastal area of intergradation appears, therefore, to be a zone in which tendencies characteristic of all three races are complexly intermingled. Whether the three named races have arisen through isolation from this stock of intergrades or whether the intergrading coastal population represents later mingling of three stocks that had earlier attained morphological separation is a question. Evidence to be cited below suggests that the latter is the more likely hypothesis.

There is little doubt that the rogersi stock was derived from the primitive advena stock, and it seems likely that r. ochlocknensis is the most primitive form of the complex. The first pleopod as well as the other morphological characters of r. ochlocknensis are very similar to those of P. advena of southwest-central Georgia. Further evidence to support the supposition that the rogersi complex was derived from an ancestral advena stock lies in the fact that advena occurs in the region of the headwaters of the Ochlocknee, and r. ochlocknensis seems to be almost confined to its drainage system in Liberty and Gadsden Counties, Florida. From this stock the two other welldefined races probably arose through isolation, and the variable coastal population of intergrades has probably arisen through later mingling of these once isolated groups. Such a history of isolation followed by remingling may be related to what is known of the geological history of this part of Florida during the Pleistocene.

According to C. Wythe Cooke (1939) in his recent study of the Pleistocene terraces of Florida, Florida was even more emergent during the interval between the Talbot and Pamlico stages than it is today. At this time it would have been possible for the ancestral ochlocknensis stock to have entered the present territories occupied by rogersi and campestris by way of the flat lands bordering the Gulf. This period was followed by the Pamlico submergence, which pushed the coastline well inland, and may well have been the isolating factor responsible for the differentiation of the three races, which were then separated by wellmarked barriers on all sides. The emergence of recent times, with the reestablishment of broad areas of coastal flatwoods suitable for occupancy by the members of the *rogersi* complex, would then account for the remingling of the stocks and the production of the coastal "intergrades" discussed above.

Under present conditions it is evident that the Ochlocknee and Apalachicola Rivers are at least partial barriers to the dispersal of these crayfishes, particularly where there are belts of well-drained soils along their eastern banks. Where such soils intervene there is no evidence of intergradation across these barriers even where the ranges are quite close together. To the south, however, where suitable habitats exist on either side of the rivers, the streams themselves evidently still act as partial barriers, since there is a definite change in the characteristics of the intergrade populations at the rivers.

Material examined.—My evidence of intergradation of the three subspecies of Procambarus rogersi is based on approximately 220 specimens collected in Calhoun, Gulf, Bay, Franklin, Wakulla, Gadsden, and Leon Counties, Fla. This listing constitutes a detailed record of the distribution of the intergrades.

BAY COUNTY: 18 miles west of Port St. Joe [U. S. Highway 98] (6-638-8a, 1 JII); 17 miles west of Panama City [State Highway 10] (6-638-9b, $1 \circ$); 20.6 miles east of Panama City [U. S. Highway 98] (5-3040-7a, 1 ♂II, 2 ♀ ♀); 6.3 miles west of Beacon Hill [U. S. Highway 98] (5-341-2, 2 J JI, 2 J JII, 1 & with eggs); 12 miles west of Beacon Hill [U. S. Highway 98] (5-341-4a, 1 JII); 16.8 miles west of Beacon Hill [U. S. Highway 98] (5-341-5a, 1 ♂I, 1 ♀ with eggs); 5.3 miles southeast of Panama City [U. S. Highway 98] (5-341-6, 4 9 9, 1 9 with eggs); 0.7 miles north of Panama City [State Highway 52] (5-341-7a, 2 Q Q); 2.4 miles north of Panama City [State Highway 52] (5-341-8, $1 \circ, 1 \circ$ with eggs); 3 miles east of Panama City [State Highway 52] $(5-341-12, 2 \circ \circ);$ 7.8 miles east of Panama City [State Highway 52] (5-341-13a, 1 9); 13.1 miles east of Panama City [State Highway 52] (5-341-14a, 2 3 31, 1 JII, 2 9 9); 1 mile south of West Bay [State Highway 10] (10-1641-6a, 1 JI)12; 1.5 miles

¹² This was a second form male when caught on October 16, 1941, and molted to first form on December 20, 1941.

north of West Bay [State Highway 10] (10-1641-7, 1 9). FRANKLIN COUNTY: Franklin-Wakulla County line [U. S. Highway 319] (6-538-11, 1 JI, 1 9); 6.9 miles west of Carrabelle [U. S. Highway 319] (6-638-2a, 2 3 3 II, $3 \neq 9, 1 \neq$ with young); 9.9 miles west of Carrabelle [U. S. Highway 319] (6-638-3, 1 JII, $1 \circ$); 3.3 miles west of Apalachicola [U. S. Highway 98] (6-638-4, 1 ♂II, 3 ♀ ♀, 1 ♀ immature); 3.8 miles west of Apalachicola [U. S. Highway 98] (6-638-6, 1 JII); 23.3 miles east of Port St. Joe [U. S. Highway 98] (5-3040-4a, $2 \circ \circ$); 5 miles west of Carrabelle [U. S. Highway 319] (5-3040-1, 3 ♂ ♂ II, 3 ♀ ♀); 12 miles west of Carrabelle [U. S. Highway 319] (5- $3040-2, 2 \circ \circ); 4.2$ miles west of Apalachicola [U. S. Highway 98] (5-3040-3, 1 9); 1.9 miles south of Sumatra [State Highway 12] (5-241-8, $3 \sigma \sigma I$, $2 \circ \circ$); 8.4 miles south of Sumatra [State Highway 12] $(5-241-10a, 1 \circ \text{with eggs});$ 15.1 miles southeast of Sumatra [State Highway 12] (5-241-11a, 1 9); 20.9 miles southeast of Sumatra [State Highway 12] (5-241-12, 1 JII); 25.5 miles south of Sumatra [State Highway 12] $(5-241-13, 1 \circ)$; Intersection of State Highway 12 and U.S. Highway 319 (5-241-14a, 3 & AI, 1 AII, 3 9 9); 3 miles southwest of intersection of State Highway 12 and U. S. Highway 319 (5-241-15, 1 9); 2.3 miles west of Apalachicola [U. S. Highway 98] (5-241-16, 1 JI, 2 J JII, 1 9); 6.9 miles west of Apalachicola [U. S. Highway 98] (5-241-17a, 2 ♂ ♂II); 11.5 miles west of Apalachicola [U. S. Highway 98] (5-241-18, 1 Jimm., 1 9 with eggs). GULF COUNTY: 5.6 miles north of Port St. Joe [State Highway 6] (4-738-4, 1 JII, 1 9); 0.5 mile west of Wewahitchka [State Highway 52] (5-341-15, 1 JI); 17.6 miles west of Apalachicola [U. S. Highway 98] (5-241-19, 1 JII, 19). LIBERTY COUNTY: Vilas (9-1835-1, 1 ♂II, 2 ♀ ♀); 2.6 miles south of Hosford [State Highway 135] (5-141-6, 2 J JII, 1 9); 4.8 miles south of Telogia [State Highway 135] (5-241-1a, 1 ♂I, 1 ♂II, 1 ♀); 12 miles south of Telogia [State Highway 135] (5-241-4, 2♂♂II, 1♀); 2.6 miles southeast of Wilma [State Highway 135] (5-241-5a, 1 ♂II, 2 ♀ ♀); 6.9 miles southeast of Wilma [State Highway 135] (5-241-6a, 1 JI, 1 JII); 12.1 miles south of Wilma [State Highway 135] (5-241-7a $2 \circ \circ).$

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NOTE

This paper was originally accepted for publication in the Proceedings of the United States National Museum, and it was cited as "in press" in my *Crayfishes of Florida* (Hobbs, 1942). Wartime restrictions, however, so delayed publication by the Museum that the manuscript was withdrawn and submitted to this JOURNAL in order that the full descriptions of the two new subspecies of *Procambarus rogersi* might appear more promptly.

I wish to acknowledge the invaluable aid of the following persons who have contributed to my work on this paper, both through help in procuring specimens and in preparation of the manuscript and figures: Dr. Waldo L. Schmitt, Profs. J. S. Rogers and T. H. Hubbell, Drs. Lewis Berner, F. N. Young, and A. M. Laessle, and Messrs. Lewis Marchand and W. L. Brudon. Dr. C. J. Goodnight kindly identified the branchiobdellids for me.

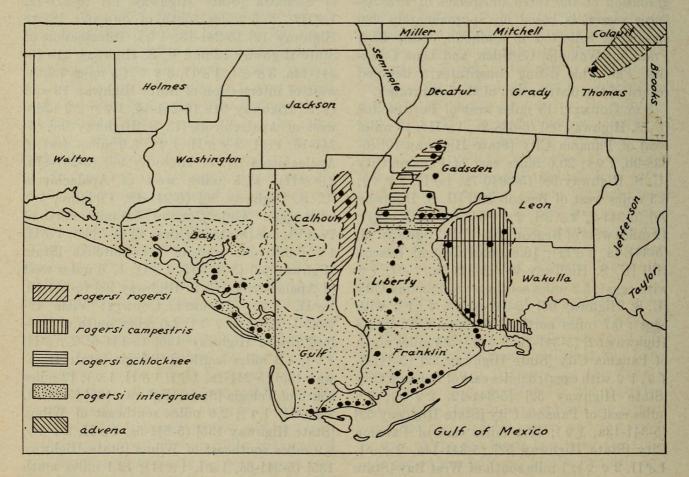


FIG. 34.—Distribution of *Procambarus rogersi* in Florida. The shaded areas indicate the extent of coastal flatwoods or low areas along streams, which seem to be available to the *rogersi* stock. The two localities lying outside of these areas in Gadsden and Liberty Counties are situated along streams that drain into the Telogia River system, thence into the Ochlocknee. The black spots represent the localities at which specimens were collected.

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