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BEHAVIORAL, MORPHOLOGICAL AND ECOLOGICAL EVIDENCE FOR TWO NEW SPECIES OF FIDDLER CRABS (GENUS *UCA*) FROM THE GULF COAST OF THE UNITED STATES[1,2]

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The fiddler crab, *Uca pugnax* (Smith) is a common form found along the Atlantic coast of the United States (Crane, 1943). The southern limit of its range on the Atlantic seaboard varies from year to year, depending upon local climatic conditions, but has been designated as Crescent Beach (Tashian and Vernberg, 1958) and Daytona Beach (Salmon, 1967), Florida. At points farther south on the east and west coast of Florida, *U. pugnax* is replaced by *U. rapax*, a closely related tropical species.

The reported range of *U. pugnax* was extended to the Gulf of Mexico by Rathbun (1918) on the basis of three specimens (USNM 2259) collected from Grand Isle, Louisiana. She remarked, however, that these individuals were morphologically atypical of forms found on the eastern seaboard. Shortly after the publication of her monograph in 1918, Rathbun examined a few individuals from Mississippi (USNM 74902) and Texas (USNM 72132) which she identified as *U. pugnax*. Salmon (1967) found morphologically similar forms on the

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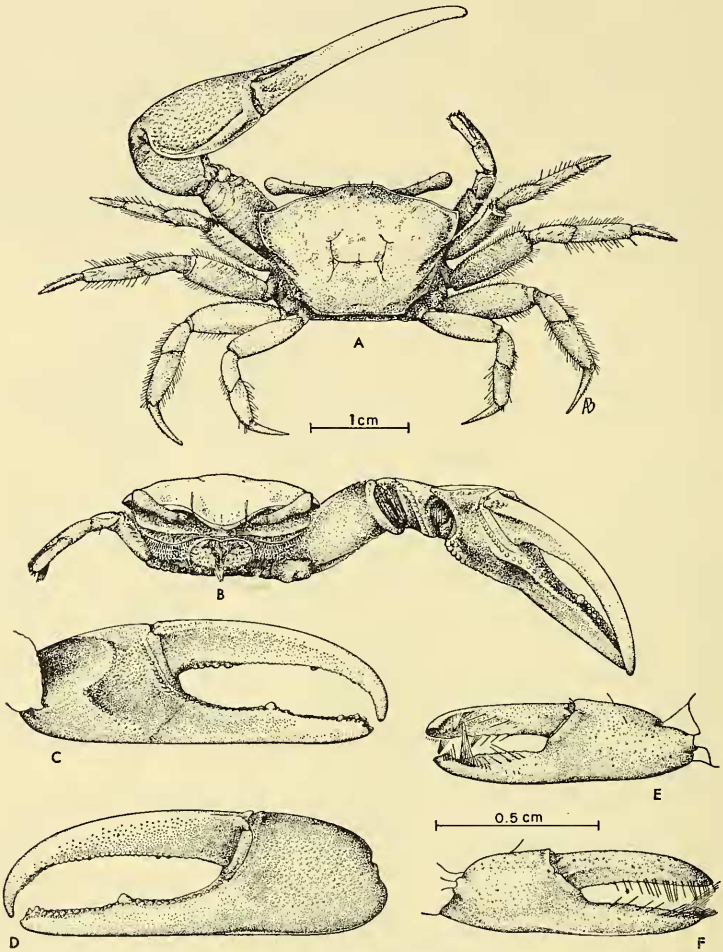

FIG. 1. *Uca longisignalis* new species, holotype male. A, dorsal view. B, front view. C, major cheliped, inner view. D, same, outer view. E, minor cheliped, inner view. F, same, outer view.

west coast of Florida at Yankeetown and farther north, but he did not extend his observations beyond the Florida coastline.

Salmon (1967), while completing a study of the display of Florida fiddler crabs, noted differences between the waving gestures of populations of fiddler crabs on the east and Gulf coast of Florida. Further, he was able to record nocturnal

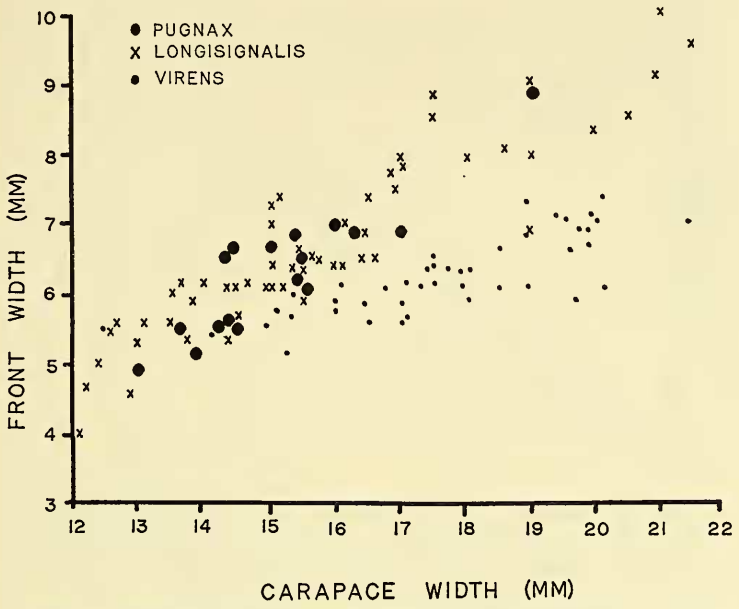

FIG. 2. Scatter plot of carapace width and corresponding front width in *Uca longisignalis* new species, *U. virens* new species, and *U. pugnax*.

sounds from males on the Gulf coast but had been unsuccessful three years previously in attempts to record these signals from North Carolina populations (Salmon, 1965). He suggested that populations of *U. pugnax* on either side of the Florida peninsula, which were geographically isolated, might be diverging into two species.

The study reported here was carried out in order to examine both Gulf and Atlantic coast populations of *U. pugnax* in more detail so that their similarities and differences in behavior and morphology could be characterized. Our results indicate that the Atlantic coast populations are distinct from those found along the Gulf coast of the United States. Further, we present evidence which suggests that the Gulf coast populations are themselves divisible into two distinct species. *Uca virens* new species, is found from Texas to Mississippi, and *U. longisignalis* new species, occurs from Louisiana to the West coast of Florida.

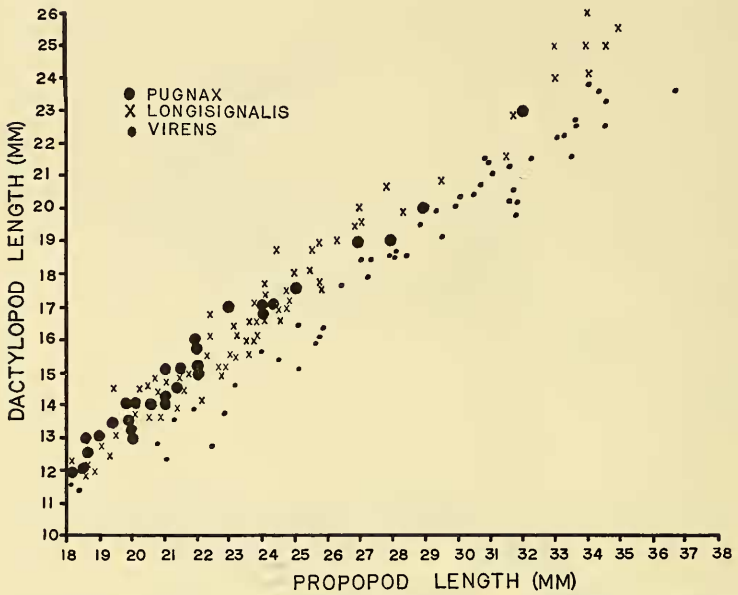

Fig. 3. Scatter plot of dactylopod and corresponding propopod lengths in *Uca longisignalis* new species, *U. virens* new species, and *U. pugnax.*

Materials and Methods

Field observations were carried out during early June, 1967 and in late August, 1966 and 1967. Gulf coast populations were studied and collected at the following localities: Port Aransas, Texas; Cameron, Louisiana; Ocean Springs, Mississippi; and Yankeetown, Florida. Atlantic coast populations were studied at Daytona Beach and St. Augustine, Florida.

The waving displays of males were filmed with a 16-mm camera and a 120-mm telephoto lens for later frame-by-frame analyses. The behavior of species showing relatively slow waving gestures was also quantified by announcing the beginning and end of the display into a tape recorder, then transcribing the data to a level recorder for measurement. The following parameters of waves by lone males were measured: general form, duration, interwave interval, and number of waves completed in a series. Air temperatures during these observations ranged from 23°–38° C.

Recordings of nocturnal sounds produced by males were made with a Uher 4000-L tape recorder at speeds of 1⅞ inches per second. Contact microphones were used for transducers, as described previously (Salmon, 1965). The temporal properties of the sounds were measured from

oscillographs made with a Fairchild oscilloscope (701) and Grass Kymograph camera (C-4) at film speeds of 25 mm/sec. The following parameters of the sounds from males were measured: sound duration, number of pulses per sound, and intervals between consecutive sounds produced in a series.

A number of morphological characters were measured in order to characterize the populations from different localities. These included the width of the front, width of the carapace as measured at its greatest dorso-lateral extension, the length of the propodus (from the tip of the finger to the proximal edge), and the length of the dactyl (from the tip of the movable finger to the upper point of articulation to the propodus). Additionally, the number, form, and distribution of the spoon-tipped hairs on the merus of the second maxilliped were examined in specimens from each of the several conspecific populations.

Distribution and Ecology of Atlantic and Gulf Coast Populations: We studied several populations of *U. pugnax* at Daytona Beach and St. Augustine, Florida. Their coloration and habitat preferences were similar to those described earlier by Tashian and Vernberg (1958) and Salmon (1967) for Florida residents.

Gulf coast populations could be separated into two forms on the basis of their distribution. *Uca virens* new species was found at Port Aransas, Texas, Cameron, La., and Ocean Springs, Miss., while *U. longisignalis* new species was found at Cameron, La., Ocean Springs, Miss., and at Yankeetown, Florida.

Differences in preferred habitat between the two Gulf forms were slight but could be recognized in the areas where the two forms overlapped. *Uca virens* new species was found in muddy sand while *U. longisignalis* new species was more common in mud and, occasionally, muddy-clay substrates. Both forms were intertidal, and both seemed to prefer the more open areas than those of dense vegetation. Habitat preferences with respect to substrate were correlated with differences in the number and form of the spoon-tipped hairs contained on the second maxillipeds (see below).

Uca longisignalis new species

Material Examined: A total of 125 specimens collected from Yankeetown, Florida and Ocean Springs, Mississippi. Holotype male, USNM 121599; paratype male USNM 122204. Type locality: Ocean Springs, Mississippi.

Etymology: Longisignalis—alluding to the extended duration of the waving display and sounds produced by the males.

Morphological Description: (Fig. 1) Carapace moderately arched and widest at antero-lateral margins. Frontal margin evenly convex. Surface of carapace smooth; H–form depression moderately outlined. Antero-lateral margins distinct, turning at obtuse angles and continuing in convergent lines to point opposite middle of cardiac region. Another

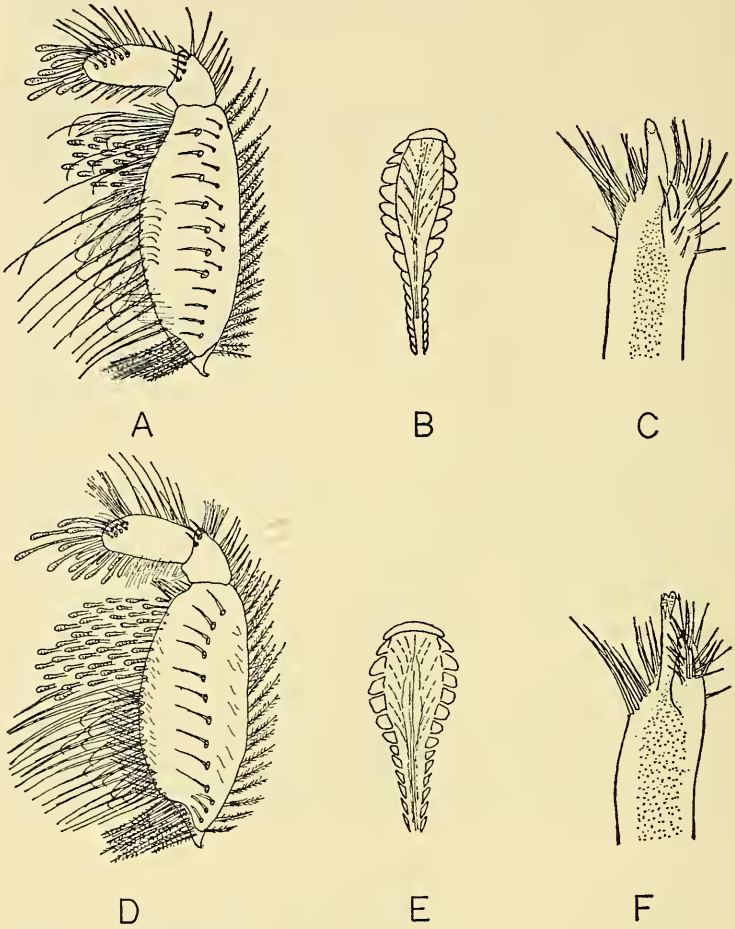

Fig. 4. *Uca longisignalis* new species. A, inner view of second maxilliped showing merus and more distal segments. B, front view of spoon-tipped process. C, inner view of tip of left abdominal appendage. *Uca virens* new species. D, inner view of second maxilliped showing merus and more distal segments. E, front view of spoon-tipped process. F, inner view of tip of left abdominal appendage. Many additional groups of bristles on maxillipeds and abdominal appendages deleted for purposes of clarity.

short ridge present on oblique margin of carapace, just above last two pairs of walking legs. Oblique margins strongly convergent, forming less than right angle when extended. Carapace about 2.3 times wider than front, but these proportions varying with size (see Fig. 2).

Minor cheliped serrated along distal two-thirds of inner margins of both fingers, except near flattened spooned tips. Fingers with distinct gap when closed. Scattered row of hairs extending along serrated margins of both fingers.

Outer surface of major cheliped smooth, but covered with many small, flat tubercles. Propodus about 1.46 times as long as dactyl, but proportions varying with size (Fig. 3). Submarginal ridge on palm weakly developed, lacking distinct tubercles and extending from proximal edge of propodus to lower margin at level below articulation with dactyl. Teeth of both fingers small; single enlarged tooth prominent near center of immovable finger. Tip of propodus blunt and obtuse, containing 4–5 prominent teeth. Inner surface of palm with oblique ridge of small tubercles, often arranged in irregular double row for short portions near pollex and extending close to lateral margin of carpal cavity.

Carpus with oblique ridge on inner surface continuing proximally along upper margin of carpus almost to articulation with merus. Ridge containing single continuous row of small tubercles.

Supplementary Specific Characters: (Fig. 4) Spoon-tipped hairs on second maxilliped totalling 25–35, arranged in 4 to 5 rows and confined to narrow zone on median inner edge of merus. Spoon-tip processes bearing 6–8 enlarged lateral lobes.

Abdominal appendages of male long, slender. Arm of appendage moderately covered with hairs. Pore opening smooth and relatively narrow.

Color: Anterior portion of carapace between eyestalks bright turquoise, blending into blue-green band posteriorly. Posterior portion of carapace dark brown to black. Major cheliped of displaying males white at tips of fingers. Inside of palm speckled with tan below and dark olive green above. Outer surface of propodus speckled olive green. Ambulatories dark brown to black. Females with less intense turquoise coloring and white chelae.

Uca virens new species

Material Examined: A total of 70 specimens collected from Port Aransas, Texas and Ocean Springs, Mississippi. Holotype male, USNM 121598; paratype male USNM 122205. Type locality: Port Aransas, Texas.

Etymology: Virens—alluding to the green band on the anterior border of the carapace.

Morphological Description: (Fig. 5) Carapace moderately arched and widest just behind antero-lateral margins. Frontal margin transverse and angulate, forming obtuse angle at either side of front. Surface of carapace smooth; H-form depression shallow. Antero-lateral margins prog-

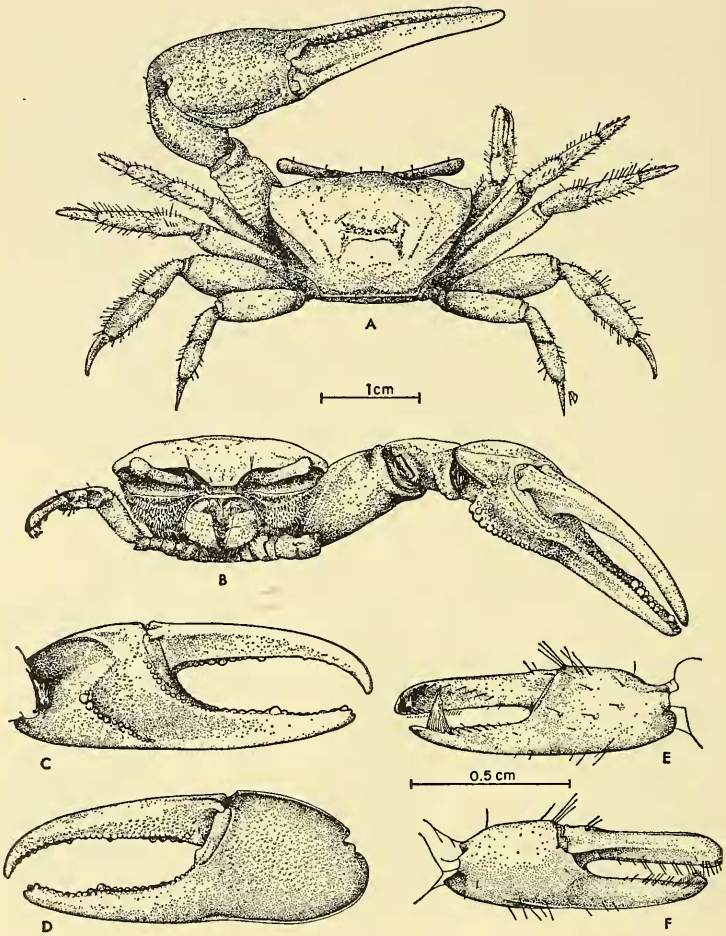

FIG. 5. *Uca virens* new species, holotype male. A, dorsal view. B, front view. C, major cheliped, inner view. D, same, outer view. E, minor cheliped, inner view. F, same, outer view.

ressively less distinct posteriorly and blending into smooth surface of carapace lateral to cardiac region. Another short ridge, just above last two pairs of walking legs, weakly developed if present. Oblique margins weakly convergent, forming right angle when extended. Carapace about 2.8 times wider than front, but proportions varying with size (Fig. 2).

Minor cheliped serrated along distal one-half of inner margin of both fingers, except near flattened spooned tips. Distinct gap present when

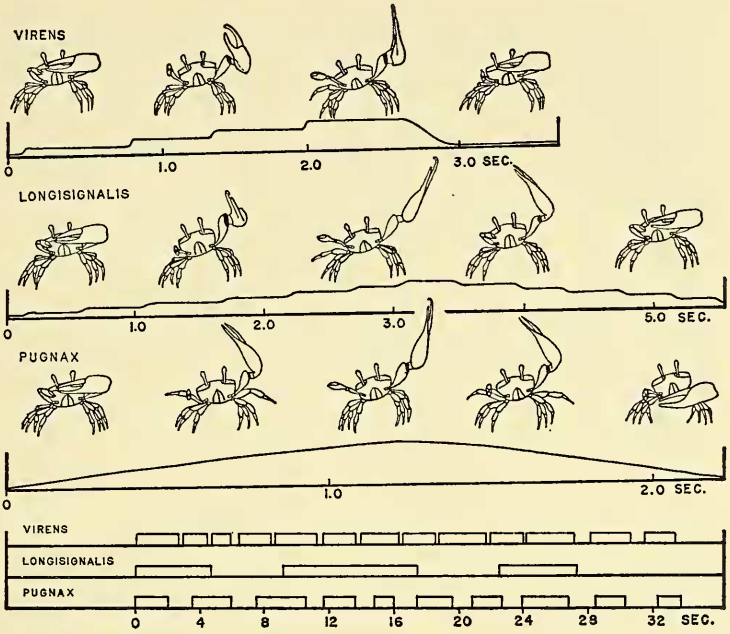

FIG. 6. Above: Topography of waving gestures displayed by males of the three species. Graph below each diagram indicates vertical position of tip of major cheliped as a function of time during the wave, with deflections indicating a "jerk."

Below: Temporal pattern of consecutive waves produced in a series by single males of each species. The deflections indicate the beginning and end of single wave.

fingers are closed. Scattered row of hairs extending along serrated margins of both fingers.

Outer surface of major cheliped smooth, but covered with many small, flat tubercles. Propodus about 1.88 times as long as dactyl, but proportions varying with size (Fig. 3). Distinct tuberculate submarginal ridge on palm, extending from proximal edge of propodus to lower margin at level below articulation with dactyl. Teeth of both fingers well developed; usually single enlarged tooth present on propodus, ⅔ of way to tip. Tip of propodus blunt and containing 3–4 large teeth. Inner surface of palm with oblique ridge of large tubercles, often arranged in irregular double row for short portions near pollex, and extending close to lateral margin of carpal cavity.

Carpus with oblique ridge on inner surface extending from lower margin, where it contains 3–8 tubercles, to upper surface; there, it con-

TABLE 1. Temporal patterns of waving display in species of *Uca* from the Atlantic and Gulf coasts.

	Location	Sample size	Wave duration (sec.) Mean	Wave duration (sec.) S. D.	Intervals between waves (sec.) Mean	Intervals between waves (sec.) S. D.
virens	Port Aransas, Texas	15 males (90 waves)	2.8	0.80	0.47	0.12
	Ocean Springs, Mississippi	6 males (54 waves)	2.5	0.62	0.43	0.08
longisignalis	Ocean Springs, Mississippi	14 males (80 waves)	5.6	1.5	4.41	2.80
	Yankeetown, Florida*	12 males (38 waves)	3.7	1.0	4.70	3.20
pugnax	Daytona Beach, Florida	6 males (42 waves)	2.3	0.31	1.40	0.70
	St. Augustine, Florida	16 males (93 waves)	2.1	0.52	1.70	1.90

* Data from Salmon, 1967.

tinues proximally along upper margin of carpus with a group of 3–8 tubercles almost to point of articulation with merus.

Supplementary Specific Characters: (Fig. 4) Spoon-tipped hairs on merus of second maxilliped totalling 50–75 and arranged in 5–6 rows. These distributed along distal half of inner edge of merus, but most concentrated medially. Spoon-tipped processes bearing 5–7 enlarged lateral lobes.

Abdominal appendages of males similar to *U. longisignalis.* However, pore opening wider and surrounded by sharp spines.

Color: Anterior border of carapace white. Anterior surface of carapace with green band, extending posteriorly over ⅓ of dorsal surface. Posterior surface of carapace deep brown. Major cheliped of displaying males white at fingers. Palm purple, outside of propodus red-brown above and blue-green at base. Ambulatories speckled dark brown. Females with brown carapace and body; chelae colored grey-white.

Rathbun's specimens (labeled as *U. pugnax*) from Texas (USNM 72132) are *U. virens.* Her collections from Mississippi (USNM 74902) and Louisiana (USNM 2259) are *U. longisignalis.*

Differences in Courtship Behavior

Waving Display: The waving display of the three forms was distinct in all populations we observed, and individuals of each form could be easily identified on the basis of these movements (Fig. 6). In *U. virens,* the major cheliped was raised vertically in 3–6 distinct jerks, then immediately returned to the front in one, or rarely, two jerks. The waves were short in duration (about three seconds) and consecutive waves were displayed with scarcely any pause. In *U. longisignalis* the waves were executed in 8–15 less pronounced jerks as the claw was raised and lowered. Each wave was rather long in duration (4–8 seconds), and there was a pause of several seconds between consecutive waves. The displays of Atlantic *U. pugnax* were executed without any jerking and, in contrast to *U. virens,* the claw was returned to the front at about the same rate as it was initially extended. Successive waves in Atlantic populations were each separated by a pause of about two seconds. The temporal properties of the waves of the three forms are summarized in Table 1.

There appeared to be little variation in the temporal patterns of waving displays within conspecific populations found in different locales. However, *U. longisignalis* observed at Yankeetown, Florida, showed consistently shorter wave durations, but no other significant deviations, than did conspecifics observed at Ocean Springs, Mississippi. The former were observed during the late summer of 1966, while the latter were studied in June during the height of the breeding season. Yankeetown forms showed displays that were often incomplete and executed at low intensity. It is quite probable that these factors account for the differences between the two populations. The values for the Atlantic

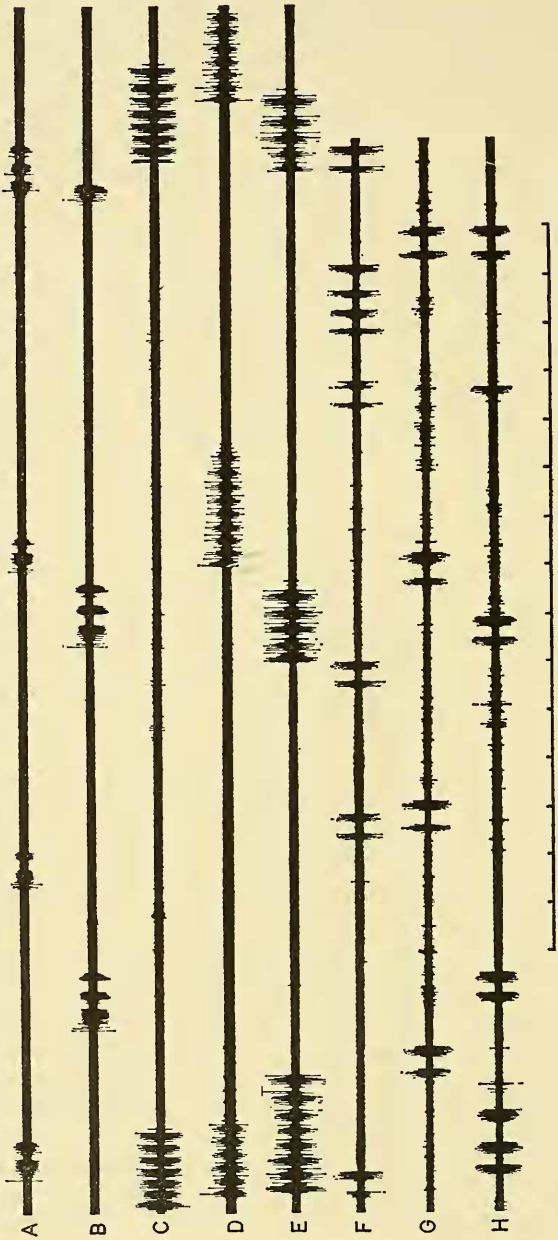

FIG. 7. Oscillographs of sounds produced by lone males at night. A and B, *Uca pugnax* at St. Augustine, Florida. C–E, *Uca longisignalis* new species at Cameron, Louisiana; Ocean Springs, Mississippi; and Yankeetown, Florida, respectively. F–H, *Uca virens* new species at Port Aransas, Texas; Cameron, Louisiana; and Ocean Springs, Mississippi, respectively.

coast forms were comparable to estimates of two seconds (Crane, 1943) and 2.5 seconds (Salmon, 1965) given for wave durations of *U. pugnax* from New York and North Carolina, respectively.

Sound Signals: Males of all three forms produced sounds during nocturnal low tides for periods of up to several hours. Males could be observed for shorter periods while producing sounds under the illumination of a flashlight. In all the crabs, the sounds were produced by movements of the ambulatory legs rather than by rapping of the major cheliped against the substrate, as described for *U. pugilator, U. speciosa,* and several other tropical species (Salmon, 1967; Crane, 1943). Sound production by movements of the ambulatories was also characteristic of *U. burgersi* Holthuis[3] and *U. rapax* (see Salmon, 1967), both closely related to *U. pugnax* (according to Crane, 1943).

Each sound, as described here, was composed of several pulses produced in a series (Fig. 7). In *U. pugnax,* the sounds were usually composed of 2–3 pulses and intervals between successive sounds averaged about 7 seconds. In *U. virens,* most sounds contained two pulses, but the intervals between successive sounds were about three seconds. In *U. longisignalis,* the sounds containing 5–14 pulses, and successive sounds in a series were each separated by long intervals (8–10 seconds). The temporal properties of the sonic signals of the three forms are summarized in Table 2.

The signals described above were all produced by lone males. Tactile stimulation by other crabs, or by touching the ambulatories of sonic males with a fine twig, elicited responses from the males typical of other species (Salmon, 1965, 1967), i.e., the stimulated males began producing sounds more rapidly and moved several millimeters into their burrows.

Discussion and Conclusions

The behavioral, ecological, and morphological characteristics of populations of fiddler crabs, heretofore designated as *U. pugnax,* indicate that these forms should be separated into three species: the nominate form found on the Atlantic coast, and two new species on the Gulf coast of the United States. The differences between the three forms do not suggest any sign of intergradation, and the forms on the Gulf coast are as distinct from one another as they are from other closely related and well established species, such as *U. rapax* and *U. burgersi.* Although we have compiled a number of lines of evidence to support our conclusions, it should be pointed out that it was the distinctiveness of the waving display of the three forms that first suggested the problem. The results of our study support Crane's (1941) original contention that these displays are species-typical movements within the genus.

In most cases, there was strikingly little variation in the morphology

[3] Specimens referred to as *U. mordax* by Salmon, 1967 are synonymous with *U. burgersi* Holthuis.

TABLE 2. Temporal patterns of sound production in species of *Uca* from the Atlantic and Gulf coasts.

	Location	Sample size	Sound duration (sec.)		Pulses per sound		Intervals between sounds (sec.)	
			Mean	S. D.	Mean	S. D.	Mean	S. D.
virens	Port Aransas, Texas	7 males (126 sounds)	0.72	0.34	1.9	0.20	3.20	2.40
	Ocean Springs, Mississippi	3 males (29 sounds)	0.74	0.36	2.1	0.20	3.00	2.10
longisignalis	Cameron, Louisiana	1 male (16 sounds)	2.40	0.50	10.4	2.00	8.40	3.40
	Ocean Springs, Mississippi	8 males (74 sounds)	2.70	0.80	9.3	3.50	10.40	4.40
	Yankeetown, Florida	2 males (38 sounds)	2.10	0.40	6.8	1.9	8.20	3.10
pugnax	St. Augustine, Florida	4 males (68 sounds)	1.14	0.20	2.4	0.3	6.7	4.20

and behavior of conspecific forms making up widely separated populations along the Gulf coast. These results are consistent with those obtained by Crane in similar studies of other species in the tropics (1941). Crane (in Tashian and Vernberg, 1958) found little evidence of variation in displays within single species throughout their range, and a noticeable absence of any tendency toward subspeciation in the genus.

All three forms are members of Crane's (1941) "Group 2" species, i.e., they have waves of rather long duration, usually executed with various degrees of "jerking." In addition, they produce sounds by movements of the ambulatories as do *U. rapax* and *U. burgersi* (see Salmon, 1967). The morphological similarities of the Group 2 species are discussed in detail by Crane (1941).

It appears that the evolution of sound production in *Uca* has developed in at least two independent lines, one including the Group 2 species, and another including *U. pugilator, U. speciosa,* and *U. spinicarpa* as well as several tropical species. The latter produce sounds by striking the base of the major cheliped against the substrate (rapping). It is likely that a detailed study of the many species of fiddlers found in the tropics may reveal other mechanisms of sonic emission. These mechanisms may be characteristics of other species groups, and should enable the formulation of a more detailed explanation of relationships and the evolution of courtship behavior in the genus, especially when combined with additional behavioral, morphological, and ecological data.

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