# ZOOLOGICA

## SCIENTIFIC CONTRIBUTIONS
## OF THE
## NEW YORK ZOOLOGICAL SOCIETY



VOLUME XXVI

Part 3

Numbers 19–27



PUBLISHED BY THE SOCIETY
THE ZOOLOGICAL PARK, NEW YORK

October 31, 1941

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19.

# Eastern Pacific Expeditions of the New York Zoological Society. XXVI.

## Crabs of the Genus *Uca* from the West Coast of Central America.[1]

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(Plates I–IX; Text-figures 1–8).

[This is the twenty-sixth of a series of papers dealing with the collections of the Eastern Pacific Expeditions of the New York Zoological Society made under the direction of Dr. William Beebe. The present paper is concerned with specimens taken on the *Arcturus* Oceanographic Expedition (1925), on the Eastern Pacific *Zaca* Expedition (1937–1938) and on a special trip made to the Pacific shores of Panama by the author in January and February, 1941. For data on localities and dates of the *Arcturus* and *Zaca* Expeditions, refer to *Zoologica*, Vol. 8, No. 1, pp. 1–32, and Vol. 23, No. 14, pp. 278–298.]

CONTENTS.



### I. INTRODUCTION.

The present study is based on three collections: It is the second paper in a series dealing with the brachyuran crabs of the Eastern Pacific *Zaca* Expedition.[2] In addition, an account is included of specimens which were taken by the author during January and February, 1941, on the Pacific coasts of Panama and the Canal Zone. Finally, a discussion is included of specimens referred by Boone (1927) to *Uca galapagensis* and *U. helleri*, since a reexamination shows that other species and fresh points of interest are involved.

[1] Contribution No. 628, Department of Tropical Research, New York Zoological Society.

[2] Previously published: Crane, 1940.

The collections comprise a total of 1,093 specimens, distributed among 27 species, of which 11 are apparently new to science. This wealth of material and the ecological observations which I was privileged to make in the field on both the *Zaca* and Panama trips, are such that considerable additions are made in this paper to our knowledge of habits, habitats and the phylogenetic relationships of the species. In the following pages all references to courtship, courtship coloration, copulation and shelter building are based on observations made at La Boca, Balboa, Canal Zone, at the mouth of the Canal, during the recent Panama trip, while reports on habitat, general habits and everyday color in life are from notes made during both the latter trip and the *Zaca* Expedition, on specimens observed and captured along the west coast from Mexico to Panama.

Certain hitherto disregarded physical characters have been found to be of taxonomic value, and while Miss Rathbun's invaluable monograph (1917) remains, as before, the foundation of any work on these species, the number of new forms in the present collection necessitated the making of a new key.

I wish to express my appreciation for aid in the preparation of this study to the following people: To Dr. William Beebe, Director of the Department of Tropical Research, for suggestions and criticism, and for granting me leave of absence to make special observations on *Uca* in Panama during the winter of 1941; to Mr. Templeton Crocker for the opportunity of collecting material while on a cruise of his yacht *Zaca;* to Dr. Waldo L. Schmitt of the United States National Museum for the loan of material, and for laboratory facilities during study trips to Washington; to Dr. Roy Miner of the American Museum of Natural History for the loan of material; to Dr. Herbert C. Clark of the Gorgas Memorial Laboratory, for laboratory facilities during my trip to Panama and to Mr. H. H. Evans for most valuable suggestions in regard to collecting grounds in Panama and the Canal Zone.

The drawings in the present paper are the painstaking work of Mr. James Butler (Text-figures 2–5) and Miss Janet Wilson (Text-figures 6–8).

## II. Summary of Important Points.

1. *Courtship:* The waving of the large claw by male fiddler crabs is without question primarily concerned with the attraction of females, at least during the breeding season, and only secondarily with the warning-off of crabs trespassing on a male's feeding range. The waving is only one manifestation, or step, in a definite courtship display or dance which varies so greatly with the species that individuals can be recognized at a distance by their characteristic motions. The other portions of the displays include raising of the body and stretching of the legs, various steps to one side or the other, revolutions, and special motions with the minor cheliped. All of these motions show off the areas of most brilliant color to the best advantage: for example, the anterior (ventral) side of the merus of the first two or three pairs of ambulatories are usually brilliantly colored in courting males, contrasting to the colored areas elsewhere on the body; yet these areas show only when the chelipeds are outstretched in display; the same is true of the merus of the major cheliped. The display of twelve species was observed.

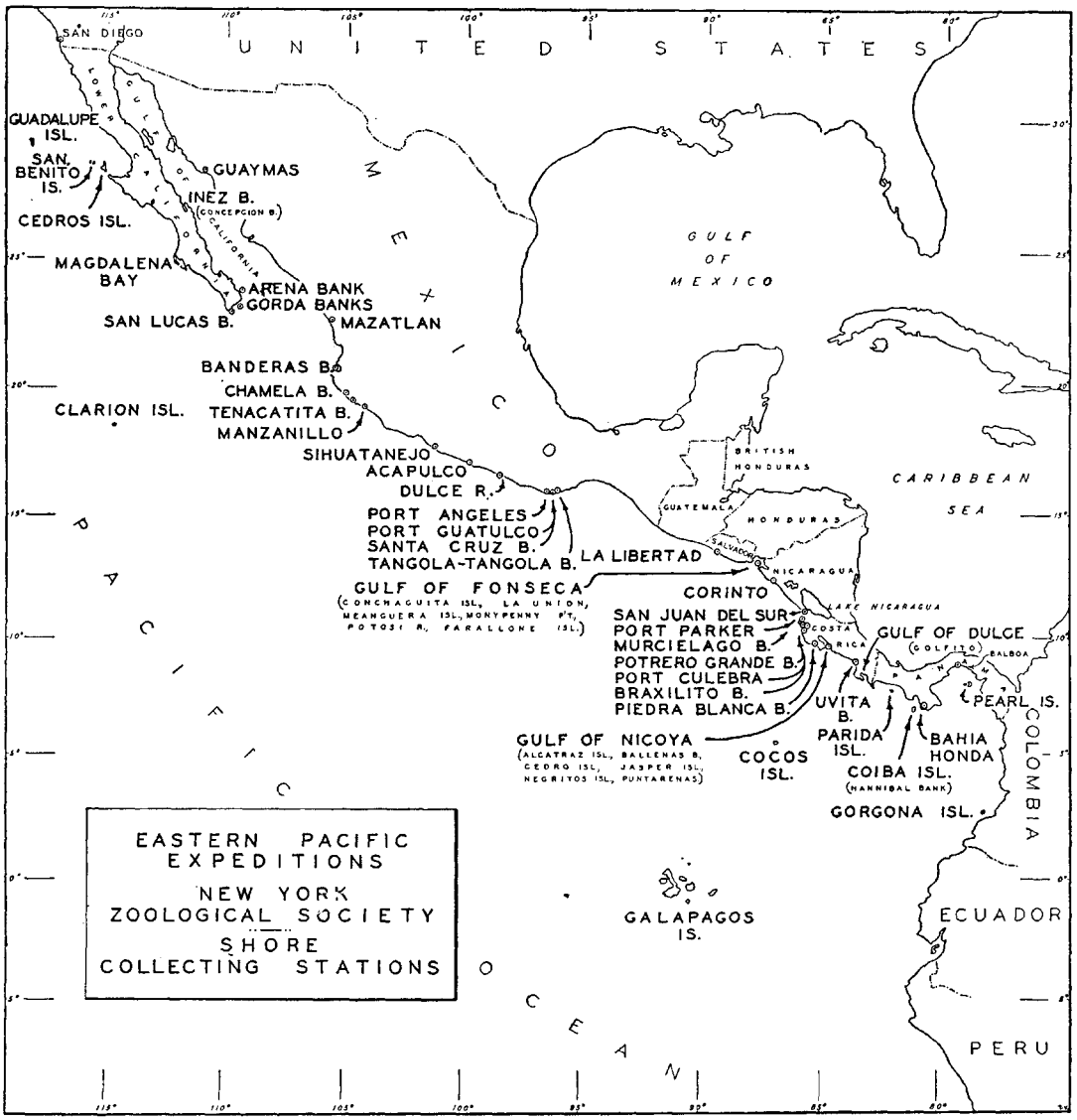
2. *Color Change:* Courting adult males, in contrast to other adult males, and, of course, to females and young, change color daily upon exposure to sunlight within the space of a short time—from a few minutes to an hour or more being required. The crab does not display vigorously and completely until full courtship color is assumed, the courting dress being always brighter than any other phase found in the same species. That courtship coloration and display play a definite part in sexual recognition and attraction is certain; that they play one also in sexual selection is likely, but has not yet been proved by experiment.

Courting males lose color rapidly when captured, resuming more or less completely the shades and patterns characteristic of the females and young, so that accurate color notes on breeding coloration can only be made when the crab is free and undisturbed. The use of binoculars in such study is almost essential.

3. *Mating:* Copulation was observed above ground, for the first time in natural surroundings, in three species. In each case it was preceded first by elaborate display of the male, and then by mutual stroking. The major cheliped played no part in actual copulation. It is thought that in most cases mating normally takes place below ground, but that when a female becomes acquiescent at the mouth of her burrow, which is usually too small for a male to enter, he induces her to mate there. When possible, however, he leads her, by means of display, to follow him down his hole. The latter procedure was observed in seven species. Even at the height of the breeding season, males are successful in only a minute fraction of their courtships, and then only after prolonged and much interrupted displaying which sometimes is protracted over a period of days. All the courtships were observed in Pacific Panama in late January and throughout February, in the midst of the dry season; ovigerous females were seen in all courting species. Whether breeding continues at other times of the year is not yet known.

4. *Shelter Building:* Shelters made of pellets of sand, roughly semispherical in shape, were built by courting males of certain species on certain days above the mouths of their burrows. The function of these structures remains as yet unexplained.

5. *Phylogeny:* A tentative phylogenetic tree of the species of *Uca* from the eastern Pacific is presented. Basic characters, including especially the mouthparts and minor chelipeds, have proved to be of more value in tracing relationships than




Text-figure 1.

Shore collecting stations of the Eastern Pacific Expeditions of the New York Zoological Society.

the characters usually employed to differentiate species, such as the form of the major cheliped, width of the front and convexity of the carapace. Related species show fundamental similarities in courtship displays as well as in physical attributes. Specialization has taken place in a number of directions, but especially toward provision for withstanding dryness, in connection with the adoption of a truly littoral existence. Species living, or at least courting, on shores which are daily exposed by the tide for relatively long periods in general have the most highly developed courtships and the brightest colors, including dazzling white, in contrast to forms living exclusively on briefly exposed mud flats.

6. *New Species:* Of the 27 species in the present collection, 11 appear to be hitherto undescribed. This raises the total of apparently valid species known from the eastern Pacific from 22 to 33.

7. *Taxonomic Notes:* Miss Rathbun's synonymy (1917) has been followed throughout. The following forms, described or recorded since that date, should apparently be synonymized as indicated:

*U. galapagensis*, Boone, 1927 (not *U. galapagensis* Rathbun) *part.* = *U. macrodactyla* (Milne-Edwards & Lucas); *part.* = *U. panamensis* (Stimpson); *part.* correctly identified.

*U. brevifrons* var. *delicata* Maccagno, 1929. = *U. brevifrons* (Stimpson).

*U. guayaquilensis* Rathbun 1935. = *U. festae* Nobili 1902.

## III. Material and Methods.

The data in the present paper are the result of two separate methods of working. The first, consisting of intensive collecting and of habitat observations from southern Mexico to Panama, was undertaken chiefly on the Eastern Pacific *Zaca* Expedition, from December, 1937, through March, 1938. Because of the nature of the trip, during which a maximum of a week or ten days was spent in each bay, and all groups of crabs were studied and collected without special reference to *Uca*, it was impossible to make prolonged and detailed observations of fiddler crab habits which by their nature require long daily periods of observation, preferably in the same locality. Therefore, during the five weeks spent in Panama during January and February of 1941, attention was directed primarily toward filling in the gaps in the *Zaca* habit notes, and only secondarily to collecting.

Observation in Panama was largely confined to one small area, a slightly brackish cove at La Boca, Balboa, Canal Zone, at the very mouth of the Canal. This locality proved to be so rich and was so accessible that it seemed wise to concentrate study here. However, colors and courtship displays were checked in other nearby places, including the mud flats at Bellavista, Panama City, and at Old Panama, a few miles south along the coast.

It was found that when the same area was visited day after day, and hours spent in observation, the activities of certain individual crabs could easily be watched for as much as four weeks at a time, individuals being differentiated by means of damaged or regenerated claws and legs, or scars on the carapace. Since many of the crabs at La Boca were, most fortunately, in the midst of courting at this time, and since my stay was definitely limited, it seemed best to make all observations on these crabs while they were in a completely natural condition, although there was a temptation to divide my time between that type of study and experiments in the field of sexual selection, to try to determine the actual extent, if any, of the effect of the male's color and display in his attraction of a mate. However, since controlled experiments to be at all significant would have required a great deal of time, it seemed better to reserve them for a later study, and to limit observation to natural reactions, particularly since this field is so little explored.

On both the *Zaca* Expedition and on the more recent trip, a pair of Number 7 Zeiss binoculars was constantly used. Although it is true that most species will overcome their fear after a few minutes and resume their activities more or less normally if an observer remains perfectly quiet close by, still the slightest motion sends them into their burrows again. On the other hand, after crabs watched through a binoculars at a distance of 12 or 15 feet have once emerged and lost their fear, it is possible to move slowly, make notes, and switch observation from one individual to another without alarming any over a period of hours.

In photographing, a Leica camera was used with a 90 mm. telephoto lens at a distance of about 20 inches. The camera was attached to a focussing device, which in turn was screwed to a tilt-top tripod head. The latter was attached to a six-inch news-camera hand-holder. The handle was thrust through a square of cardboard as far as the tripod head, in order to protect the camera from sand, and then pushed into the muddy sand up to the cardboard. A pencil stuck into the ground beside the desired crab hole was used as a temporary focussing point. After the crab emerged it was often possible, if the first exposure was not made for several minutes, to release the shutter and wind the film for another picture without alarming the crab, provided that the movements of the fingers were exceedingly slow, and hidden as much as possible by the camera. In bright sunshine, on the dark gray muddy sand of La Boca, an exposure of 1/60 of a second at F16 on Eastman Super-XX film was found to give the most satisfactory compromise between speed and depth, although even this combination gave, of course, very little depth and yet would not stop the motion of the large claw when on a downward or upward swing. A series of these photographs was found to be valuable in showing the relative position of the various appendages at a given point in the display in the various species, and proved a most useful addition and check to repeated visual observations.

Methods of measurements and special terms used in the following pages should be defined thus:

1. *Length.* Measured from most anterior extension of front to posterior margin of carapace, in the longitudinal median line.

2. *Length of palm.* In either major or minor cheliped, measured from its most proximal origin on external side to the gape between the chelae, midway between lower base of dactyl and upper base of pollex.

3. *Base of palm to tip of pollex.* Measured from most proximal point of base of palm on external side to tip of pollex.

4. *Length of dactyl.* Measured from its origin on dorsal profile to its most distal projection.

5. *Width of front.* Measured between posterior margins of bases of eyestalks, as they appear when the eyes are lying flat in their sockets.

6. *Major side.* The side giving rise to the large or major cheliped.

7. *Minor side.* The side giving rise to the small or minor cheliped.

8. *Eyebrow.* As defined by Miss Rathbun (1917, p. 375); the intervening space between the two margins of the upper part of the orbit; it is usually broad, more or less inclined, roughly triangular.

9. *Suborbital region.* The area between the

lower border of the orbit and the pterygostomian region.

10. *Grooving of ischium of third maxillipeds.* This character is best examined with the appendage held out of liquid, and turned back and forth under a good lens in a strong, oblique light.

11. *Number of spoon-tipped hairs on second maxilliped.* Throughout the following study, where the number of spoon-tipped hairs is referred to, the count given is of those on the merus of the second maxilliped only; that is, those which occur on the tip of the palp are excluded. In those forms with most of the internal (upper) surface of the merus lined with these hairs, only those individual hairs are counted which project beyond the inner margin; the number of rows of hairs given, however, is always the total number. In all counts, hairs with rudimentary spooned tips are disregarded.

12. *Display.* The unit of behavior consisting of a single wave or gesture with the major cheliped along with its associated activities (stretching, running, "dancing," rapping, etc.). A number of displays following quickly upon one another, with little or no pause between, is termed a "series."

## IV. Ecology.

### A. Habitat.

In general, the habitat of individual species is much restricted; some forms are found only in open sun on brackish salt mudflats, others in the deep shade among mangrove roots, still others on open muddy sand beaches, and so on. A given type of terrain may be expected to yield certain species; a similar but slightly different type only a few yards away, supports other forms. Some species, however, may inhabit more than one kind of environment. The great majority live in mud, either on protected tidal flats close to the mouths of streams, so that the water is somewhat brackish, or on the banks of sluggish streams of brackish water. Probably species originally migrated from this relatively stable, quiet environment to fresh water streams on the one hand and to open marine beaches on the other. The habitats of species in the present collection are as follows:

1. Muddy banks of fresh water streams (mostly shaded).
   *pygmaea*
   *zacae*
   *brevifrons*
   *mordax*
   *latimanus*

2. Muddy banks of brackish streams (mostly shaded).
   *mordax*
   *brevifrons*
   *limicola*
   *latimanus*

3. White clay banks of brackish streams (mostly shaded).
   *argillicola*

4. Mud, among mangroves (completely or partly shaded).
   *zacae*
   *mordax*
   *brevifrons*
   *tomentosa*
   *umbratila*
   *inaequalis*
   *tenuipedis*
   *batuenta*
   *crenulata*

5. Mud, among unshaded mangrove shoots.
   *insignis*
   *oerstedi*
   *batuenta*

6. Tidal mud flats (unshaded).
   *princeps*
   *heteropleura*
   *stylifera*
   *insignis*
   *macrodactyla*
   *oerstedi*
   *inaequalis* (rarely)
   *saltitanta*
   *beebei* (near beach)
   *galapagensis* (?)
   *helleri* (?)

7. Protected muddy-sand flats or beaches (unshaded).
   *princeps*
   *heteropleura*
   *stylifera*
   *insignis*
   *beebei*
   *stenodactyla*
   *deichmanni*
   *latimanus*
   *terpsichores*

8. Marine sandy beaches, among stones.
   *panamensis*

There is evidence (see page 170ff.) for the belief that *U. princeps*, *heteropleura* and *stylifera* spend most of their time on mud-flats, but come to adjacent sandy-mud beaches to court, since the added firmness of the ground would probably be a distinct aid to display.

La Boca: As an example of a particularly and surprisingly rich locality for the study of fiddler crabs, a small cove on the left bank of the Pacific mouth of the Canal is unsurpassed. This cove, lying between the Balboa docks and the La Boca ferry, and surrounded by piers, motor roads and the continuous traffic of the Canal, yielded 15 species of *Uca* in January and February, 1941, in an area not more than 600 feet square. The total number of individuals in this space must have run into the hundreds of thousands. Of these species, 12 were actively courting. The cove is entirely empty of water at low tide, exposing a mud flat and, bounding it on two sides, a narrow beach of muddy sand. At the inner end, the muddy sand is mixed with gravel, and adjoins a small clump of mangroves.

The third side, parallel to the Canal, is bounded by Pier No. 4, and the fourth side, facing the canal mouth and the ferry, is open. The water is slightly brackish, because of the overflow from the canal locks. The exceptional richness is probably due chiefly to the fact that a large sewer opens practically into the cove, and that garbage from ships is frequently washed up. The dissolved organic detritus from these sources must greatly enrich the tidal deposits on the mud. The fact that these 15 species taken included 5 hitherto undescribed (although all of them had been taken also on the *Zaca* Expedition, farther up the coast) shows how many valuable studies are waiting to be made in the tropics, even in the most accessible, thickly populated and apparently unlikely areas.

The extent to which more than one species occupies a given stretch of ground seems to depend entirely on the available space and the number of individuals it can support, provided of course that the terrain is equally suitable for the various species. At La Boca, for example, in one part of the beach *stenodactyla* was dominant, but mingled with numerous *beebei* and rare *stylifera;* farther down toward the mud, where the ground stayed more moist, were found *deichmanni*, *heteropleura*, and, dominantly, *beebei*. In the most protected part of the cove, most subject to dryness, behind the mangroves, *latimanus* was dominant, with only very few *terpsichores* intermingled; in the gravelly sand area, *beebei* was dominant, mingled with uncommon *terpsichores*. In less rich areas, the species tend to keep separate, there being definite boundaries, for example at Corinto, Nicaragua, between a large colony of *stenodactyla* and an equally large one of *stylifera* close by, on apparently identical terrain.

In crowded colonies, with the feeding ranges of individuals much restricted, there are of course many more provocations for fighting than in uncrowded areas, but it also seems that far more toleration has been developed in these individuals. Sex obviously is an important if not vital factor in argument. Adult males of different species and the same or different sizes will tolerate each other's burrows exceedingly close together: *beebei* and *stenodactyla* have been seen living day after day only one and a half inches apart, whereas adult males of the same species will tolerate each other's burrows not less than three inches apart and generally more. Females and young crowd closely, likewise, with practically no argument.

## B. Burrows.

No special studies were made on the subject of burrow digging, except to determine average depths and forms for the various species. As was to be expected, species on yielding mud had the shallowest holes, and large species high up on relatively dry muddy sand beaches, or along the banks of drying streams, dug deepest. The burrows of individuals of the same species varied considerably, depending on their location and, of course, on the size of the crab. The instinct of burrow-making seems least well developed in *panamensis*, which lives on the stone-strewn ends of sandy beaches. Very young crabs of all species do not dig, but run freely in and out of the burrows of adults, both of their own and different species, which pay no attention to the small ones whatever. For detailed accounts of burrow digging, consult especially Pearse (1912), Dembowski (1926) and Verwey (1930).

An interesting point is that *stylifera* and *beebei*, at least, often occupy their burrows for days and even weeks, without changing the location of the mouth by so much as half an inch. Contrary to Dembowski's observations on *pugilator* in captivity, in all the species observed the crab emerged after high tide, leaving the entire length of the burrow free, and frequently did not repair or change it at all from one day to the next. The crab must simply push its way through the sand in emerging, instead of digging himself out in such a way that a hole only the size of himself is left at the top, as seen by Dembowski.

Burrows are usually, but not always, plugged up before the tide covers them. Females and young, especially of *latimanus*, which lives at La Boca high on the shore, often plug their holes with a dome of pellets brought up from below for two or three hours around noon on especially hot, bright days; later, if the tide is still far out, they reemerge and resume feeding.

## C. Feeding.

The general process of scooping up mud or sand with the spooned minor chelipeds, carrying it to the mouth, separating the organic particles by poorly-understood actions of the mouthparts and passing the remaining detritus out at the posterior end of the buccal cavity in the form of a pellet, has been too well stated previously to need repetition. The observations of Pearse (1912), Monod, and Verwey are the most detailed. The method by which the actual sifting is done remains as mysterious as ever.

Every species observed on the west coast definitely wiped or clipped off the pellet which formed at the posterior part of the buccal cavity after between 6 and 16 cheliped-fuls of sand or mud had been conveyed to the mouth, and carefully placed the pellet in front or to one side of the crab; the only exceptions were a few individuals observed starting to feed while there was still some water on a mudflat as the tide was going out; in these cases the water dissolved and carried away the rejected mud. Matthew's statement that *U. leptodactyla* on the coast of Brazil picked up separate organic particles from the ground is most interesting; it seems likely that there was an error made in observation; the same is almost certainly true, as Verwey has contended, of Symon's statement that the rejected mud passed out at the *front* of the buccal cavity. Altogether, I have watched at least 20 species of *Uca* actually feeding, and in all the process is identical, save for three exceptions. The first, that of *Uca's* feeding with the mud

slightly underwater, has been noted; the second was that of four individuals of *brevifrons* seen feeding on mammalian excrement on the bank of a fresh-water stream, several miles from the coast, at Port Parker, Costa Rica; the third is the practice of *panamensis* of frequently climbing upon rocks and scraping off the algae for food with its small cheliped, just as do *Pachygrapsus transversus*, *Grapsus grapsus*, and others. Both *brevifrons* and *panamensis*, however, also feed in the usual fashion of fiddler crabs. Although there are doubtless exceptions, like the *brevifrons* mentioned above, and those noted by Pearse (1912), fiddlers as a general rule are certainly not scavengers: a number of times I have seen garbage, dead fish, or a dead bird in all stages of freshness and decomposition washed up in a colony of fiddlers and lying untouched in their midst, although normally-nocturnal hermit crabs were swarming over it.

The roles played by the various types of minor chelae and the various numbers of spooned and wooly hairs on the second maxillipeds are unknown; they will be further discussed on pages 161 to 165.

### D. Fighting.

The conclusions of most other observers were verified that, although brief duels, in which the large chelae are interlocked, are frequent, injury is exceedingly rare. I have only once seen any dismemberment actually take place, and this was the extreme tip of a dactyl. However, the frequent sight of crabs with similarly or further damaged chelae indicates that such mishaps do occur now and then, although, of course, it is possible that they can also occur in other ways, such as by being broken on a stone against the side of the burrow, or in escaping from an enemy.

A definite duelling ritual was followed in all except cases of extreme provocation, such as pursuit of the same female in *U. stenodactyla*, in which there was no time for preliminaries. Usually, however, a duel proceeded as follows: *Only infrequently* was a duel preceded by display, —i. e., by rhythmic series of beckonings—and then never by vigorous display such as was used in courting a female. Instead, the combatants first prance toward each other, stiff-legged, patting the ground with the bottom of the great palms and claws, as though in challenge. Then both lunge and feint a few times, with the back and sides of the semi-flexed chelipeds, which meet in audible clicks. At last, after several or half a dozen such parries, they proceed to the last step and interlock claws. This last movement is always undertaken warily, since there is always danger that the nipper may be damaged or wrenched off. Then, the claws locked, the crabs lunge in turn, pushing each other back and forth, first one and then the other sinking down and back until his shell often actually touches the ground. Usually this continues until the weaker breaks away and runs for his hole; occasionally he is somersaulted backward with a flip of his opponent's claw; often the larger simply stops fighting and moves off without there being any decision. Most duels last only a few seconds; the record was 25 minutes (see p. 160). Sometimes, as has been observed by others, the weaker is pushed down his own hole, where he uses his large claw to stop up the opening, for a few minutes, apparently to prevent the entry of his antagonist.

The provocation for a fight is usually either poaching on the territory of another male, or courting of the same female. Sometimes, however, there is no stimulus apparent for the most spirited encounters; until some better explanation is found, these must be laid to sheer excess energy, probably associated with the condition of the glands in the breeding season, or may simply be termed sport (see p. 159).

### E. Crippled Crabs.

Several instances have been observed where crabs with badly damaged chelae, with the cheliped completely missing, or with more than two ambulatories missing, were definitely bullied by other crabs. In each of these cases the cripple was repeatedly driven down his hole by one of his neighbors. Once a normal male *U. beebei* kept watch for at least several hours over an injured neighbor, the burrow of which was a foot away, well beyond the feeding ground of the normal crab. Every time the cripple emerged the neighbor would stop his own feeding or courting, run over and struggle until the cripple retired to his hole, after which the normal crab would push sand in after him and stamp it down until no trace of the burrow was left. Each time the cripple emerged the routine was repeated. No attempt appeared to be made actually to harm the crab or to follow him down his hole.

Many crabs with claws in various stages of regeneration, however, seemed to carry on completely normal lives. Twice I have seen crabs with the *minor* cheliped missing which were eating awkwardly, but with apparent success, with the major cheliped. I have not yet observed a male without the major cheliped temporarily mistaken for a female as described by Verwey. For a case of a male courting with a half-regenerated claw, see p. 155.

### F. Display, Coloration and Shelter-Building: Their Relation to Courtship.

For more than a hundred years the sexual dimorphism of fiddler crabs, the function of the waving of the large claw in the air, the frequently brilliant color of the large claw and the possible significance of all these factors in regard to sexual selection, have become matters of increasing interest and controversy to students both of crustacea and of general evolution. The opinions of the principal workers in the field may be briefly summarized as follows: The earliest—Müller (1869, 1881), Darwin (1871) and Alcock (1892, 1902)—were convinced that both waving and bright colors played a definite part in courtship, that females recognized males in this fashion

and appreciated the display, which gave to color and activity a vital role in sexual selection. Pearse (1912, 1914.1, 1914.2) accepted the conclusion that the males danced around the females in order to attract their attention, but was not convinced that the females were thus attracted, or that the colors had anything to do with sexual selection. Symons (1920), Johnson & Snook (1927), Beebe (1928) and Matthews (1930) added brief observations on various species which showed that males were sometimes definitely stimulated by females to increased waving activity and special behavior. And, finally, Verwey (1930) and Hediger (1933, 1934) denied that the waving had anything whatever to do with courtship, declaring that it was carried on instead solely to designate the possession of a hole, and limitation of the surrounding feeding area.

After concentrated observation in Panama during the breeding season of a dozen species living in a single restricted area, I am convinced that the truth lies somewhere near the middle of these extremes of conflicting opinions. Waving, as in other crabs, is certainly carried on some of the time as a warning to other males and to delimit territory in some (but not in all) species of *Uca*. On the other hand, in many, if not in all species, waving definitely plays a large part in courtship and, in one species at least (*latimanus*), is apparently carried on only by courting males.

In regard to the importance of color in waving, I cannot draw definite conclusions until further studies have been carried out. These must include experiments in artificial coloration as well as many more observations on the natural behavior of the crabs. However, it seems certain that color and motion are correlated in display, although color is perhaps the less important of the two aspects. This subject will be further discussed later (pp. 154 to 159).

*Display Activity:* A comparison of the observations of the authorities listed above shows that among different species there are certain variations in the activities accompanying waving. Studies on Philippine fiddlers by Pearse (1912) show that in one or more species the males dance around the female, showing only their backs to her, so that the great chelae could not be seen by the females, which usually paid no attention to the males in any case. Sometimes the males held statuesque poses, the chelipeds upraised or outspread for minutes at a time; the females often were, surprisingly, more brightly colored than males of their own species. Pearse states, however, that his observations were not made during the breeding season, and season should doubtless be held a most important factor in all studies of display and coloration among these crabs.

Alcock, reporting on *annulipes* in Ceylon, Symons on an unidentified *Uca* on the same island, Johnson & Snook on *crenulata* in California and Matthews on *leptodactyla* in Brazil, all reported that the males of these particular species were galvanized to more active waving by the appearance or presence of females. Johnson & Snook stated definitely that this reaction took place during the breeding season, and that crabs did not wave in captivity, although they carried on all other normal daily activities.

Beebe, observing *mordax* in Haiti, found that certain females stimulated the males to intensified waving, which consisted of "a beckoning in five jerks, the last of which almost threw the crab over on its back; the difference between this gesture of the right hand of passionate fellowship and that of shaking the fist in the face of any passing male was hardly to be discerned. In the case of courtship the fiddler would often freeze into a statuesque pose for three or four minutes at a time."

Swartze & Safir observing *pugilator* in Massachusetts, and Hediger studying *tangeri* in Morocco, agreed that the crabs waved at the rate of once every two seconds; *pugilator* varied simple waving with statuesque poses according to Pearse (1914.1) such as those in *mordax* and some of the Philippine crabs (Pearse, 1912). Hediger mentions no posing in *tangeri*, however, but refers to the elevation of the whole body which sometimes accompanies beckoning.

Verwey, in his study of *Uca* in Java, reported that *signata* in waving, stretched high up and sank back, sometimes shaking all over. This species, according to the same author, when captured as well as when in the field, waved threateningly at both males and females, though apparently not so forcefully at the latter sex. Although Verwey witnessed no copulations, he saw males approach and cover females from behind, giving the females no opportunity to recognize, much less be attracted, by the male in question. He was apparently present during the breeding season, since he has a number of records concerning the abundance of ovigerous females on various dates.

The observations summarized above show that waving, whether or not the observer admits its being used in courtship, is often accompanied or varied by the following activities: (1) by statuesque posing with the arm outstretched or upraised, (2) by shaking of the entire body, (3) by elevation of the body with each beckoning gesture, (4) by "dancing" around the females, and (5) by increase of tempo in the presence of females.

My own observations show that the last characteristic of accelerated waving is the only one which is characteristic of most species in display. In Panama, each of the species studied combined with waving variations of one or more of these five and other activities. In fact, *each species proved to have a definite, individual display, differing so markedly from that of every other species observed, that closely related species could be recognized at a distance merely by the form of the display. Furthermore, related species had fundamental similarities of display in common, and series of species, showing progressive specialization*

*of structure, in general showed similar progression in display.*

At La Boca, Balboa, Canal Zone, the courtships of twelve species were studied in considerable detail. These twelve are divided into three groups, each composed of more or less closely related species. The first ("Group 1," p. 165) consists of *princeps*, *heteropleura* and *stylifera;* the second ("Group 4," p. 166) of *oerstedi*, *inaequalis*, *batuenta* and *saltitanta;* the third ("Group 5," p. 166) of *beebei*, *stenodactyla*, *deichmanni*, *latimanus* and *terpsichores*. In this last group the first two and the last three form definite subgroups.

The display of a thirteenth species, *panamensis*, was seen only once, and on this occasion the crabs were apparently not displaying fully; hence it is omitted from this summary, but described on p. 204.

The basic element in all fiddler display is, of course, "waving" or "beckoning" with the major cheliped. In its simplest form this consists of unflexing the manus and chelae from the resting position in front of the mouth, by movements of the ischium, merus, and, perhaps, carpus, which elevate the distal elements diagonally over the head; they are usually lowered at once, without a pause, often with a jerk, in the same plane to the original position. The variations of this simple beckoning gesture and its accompaniments in the twelve species listed above are as follows:

1. *Beckoning or Waving:* a. Three of the four crabs of the second group hold in common a special sort of cheliped motion: After the usual beckoning, the cheliped is brought to the ground, flexed, more or less in front of its usual rest position, and is then bounced back into place with three or four raps of the ground; this additional action is added to the regular display occasionally in *inaequalis*, often in *batuenta* and always in *saltitanta*. In the latter species the cheliped is bounced vigorously almost in place, since only rarely does it fall in front of its normal rest position. In physical characteristics also these three species show progressively greater specialization.

b. *U. deichmanni* holds the cheliped for an instant at the highest point of its reach, then lowers it into position and raises it again without a pause, so that the accent comes at the peak of its stretch, instead of in the flexed rest position.

c. *U. latimanus* makes a somewhat circular gesture in beckoning. To a lesser degree this is occasionally true of other species.

d. *U. terpsichores* starts display with the manus and dactyl of the large cheliped half unflexed, pointing straight out in front of the crab.

e. The rate of display when the crab is not specially excited varies among species from two or more gestures to the second with no pause between them (*saltitanta*, *beebei*, *deichmanni* and *terpsichores*) to one and a half to three seconds being required for every display, including both the gesture and the pause following it (*princeps*, *oerstedi*, *inaequalis*). Both slow and fast displays occur in all groups, without relation to the degree of specialization.

Usually a more or less definite number of displays is made in a series when a given species is displaying fully, each series being followed by a rest of seconds or minutes. The most tireless so far observed is *saltitanta*, which frequently displays, at the rate of two gestures to the second, for upwards of one hundred at a time without an instant's pause. After a rest of several seconds another equally long series will be commenced, and the procedure may continue, without interruption for true rest or feeding, for at least an hour. On the other hand, in every species display is often casual, half-hearted and punctuated by feeding.

2. *Elevation of Body during Beckoning:* As in *tangeri*, the body is elevated and depressed during each beckoning by *princeps*, *heteropleura*, *stylifera* (sometimes), *inaequalis*, *batuenta*, *saltitanta* and *deichmanni*. The other five species hold it consistently high during a series of displays. In elevation, the crab stretches to tip-toe with the raising of the cheliped, and sinks into position when it is lowered. *U. heteropleura* carries this habit to the greatest extreme, stretching so high that only the tips of the two middle pairs of ambulatories remain on the ground. *U. stylifera* sometimes stretches the two front ambulatories, elevating the anterior part of the carapace, and simultaneously flexing the posterior legs, so that the rear part of the body is lowered during a display; this variation does not depend on the added stimulus of a female, but may be inserted in the midst of a series of displays, or an entire inter-tidal period may be devoted to this variety. Species which elevate and depress the carapace during each display occur in all three groups.

3. *Position of Chelae:* The chelae of both major and minor chelipeds are usually held slightly open and parallel during a series of displays; sometimes, however (especially in *batuenta* and *saltitanta*) they are opened and closed with every display—opening wide on the upward swing of the large cheliped and closing on its descent.

4. *Motion of Minor Cheliped:* Often the minor cheliped is moved in a feeble imitation of the beckoning or outward spreading of that of the major. This is generally true of *princeps*, *heteropleura*, and *terpsichores*, and true under conditions of excitement in other species.

5. Some species remain in one spot during display, notably *heteropleura*, which stretches up on its two middle pairs of ambulatories. More, however, usually take several steps to one side or the other with each elevation of the cheliped; in a given series of displays, they usually move several times in the same direction, then back to the starting point beside the hole; or with one gesture they may move to the right, with the next to the left. There is considerable leeway of behavior within a species in this activity, and individuals show similar variation in their behavior from hour to hour or day to day. *U. oerstedi* tends to move right around its hole, facing always outward, when the attention of a

female is not involved, during a series of displays. In the highly specialized courtship of *stenodactyla*, the males chase the females with the arm outstretched, motionless, or held overhead. If they can manage to approach a female closely enough, they surround her loosely with the cheliped, and race with her over the beach, apparently trying to maneuver her to their holes (for details see p. 196).

6. *Revolution:* The only instances I saw of a crab dancing with his back to a female were all performed by individuals of a single species, *beebei*. In this crab the anterior part of the carapace is a brilliant iridescent green, the cheliped chiefly rose, ochre and plum-colored, the anterior parts of the ambulatory meri magenta. Males of this species in a number of cases almost always revolved before females whose attention they had captured. The color of the carapace in this relatively dull form was certainly to human eyes at least as striking as that of the cheliped, and the combination most effective.

7. *Special Effects Reserved for Later Stages of Courtship:* The usual acceleration in tempo of display during active courtship of interested or potentially interested females has already been noted. In addition, special actions, highly characteristic specifically, may be observed in the later stages of courtship. Probably many more will be added to the following list when the complete courtship of each species is known.

a. *U. oerstedi*, when actively courting a female, vibrates the brilliant blue anterior ambulatories when the chelipeds are outstretched.

b. *U. saltitanta*, when convinced that a female is ready to follow him down his burrow, pauses halfway down its mouth, extends the ambulatories of the major side rigidly in the air and vibrates them rapidly.

c. *U. latimanus* vibrates the minor cheliped rapidly when displaying before an interested female. *U. stenodactyla*, when pursuing a female, extends this appendage stiffly outward, the chelae wide open, corresponding roughly to the gesture made with the large cheliped at this time.

d. *U. terpsichores* sometimes adopts the statuesque pose previously noted in Philippine species (Pearse, 1912), in *pugilator* (Pearse, 1914.1) and *mordax* (Beebe, 1928), standing before a female for seconds at a time with the major cheliped spread out rigidly sideways; this pose in the present species is never held longer than a minute. *U. stenodactyla* extends the major cheliped similarly, either sideways or upward, when chasing females.

e. Special steps with the ambulatories, giving the effect of a definite dance, are taken in the last stages of courtship by two quite unrelated species, *stylifera* and *terpsichores*.

f. Mutual stroking of legs and carapaces with the ambulatories by both male and female took place in the final part of courtship in all three species in which copulation was observed, namely *stylifera, beebei* and *stenodactyla*. In each case the male instigated the stroking and was by far the more active partner.

8. *Use of Special Display Ground:* All species, when courting, in general keep the ground surrounding their holes well packed down and free of feeding pellets, but *saltitanta*, which lives and displays on the stickiest, dampest mud flats, whenever possible mounts to the summit of a nearby elevation, sometimes a dozen times his own height, in order to display.

9. Although particular attention was given, no hint was seen of the use of antennae, ocular stylets (in *heteropleura* and *stylifera*) or of stridulating ridges (in *terpsichores* and allies) in display.

*Coloration:* As has been repeatedly noticed, the adult males in the genus *Uca* are frequently brilliantly colored, especially in regard to their large cheliped. The females and young on the other hand are relatively dull, being usually brown or gray, often spotted or mottled with darker or lighter. Pearse (1912) alone has remarked that "at Manila the female fiddlers often were, to the human eye, more brightly colored than males of their own species, and the female's bright colors were on her back and legs so that they could readily be seen by a male dancing behind her, but *she* did no dancing." As the author remarked, his observations were not made during the breeding season.

Müller, observing a species of *Uca* in Brazil, was apparently the first to notice color change in the field, of which no further accounts seem to have appeared until the present study.[3] His summary (1881, p. 472) is as follows: "When it (the fiddler) runs from its moist burrow into the sunlight the entire splendor of its nuptial clothes develops; as soon as one catches it, the pure white, the light green, which decorate its claws, begin to lose their luster and change in a few minutes into uniform gray." The present author, unfamiliar with the above reference when making observations in Panama, found exactly similar

[3] The interesting observations made on Atlantic fiddler crabs from which the eyestalks have been removed are not directly relevant to the present study, since all were made under extremely unnatural laboratory conditions. The most recent summary (1940) of Abramowitz & Abramowitz indicates that eyestalk removal brings about loss of pigment, accelerates moulting, increases the death-rate in moulting and results in gigantism. The authors also insert the following remarks (p. 187) without further elaboration, regarding the breeding of *U. pugilator* in captivity: "*Uca* breeds during September, as indicated by the appearance of large masses of eggs, copulation and final shedding of the eggs. Animals without eyestalks have been observed to copulate and shed their eggs. However, such animals were blinded for only a few weeks before the onset of the breeding season, and thus sufficient time may not have elapsed for any effect on reproduction to take place. This is worth investigation, however, for as yet no endocrine influence on the reproductive system of crustaceans has been demonstrated." Brown concluded (1940) that the source of the chromatophorotrophic substance of the crustacean eyestalk, including that of *Uca*, is the sinus gland. Kleinholz [& Bourquin (1941), however, state that not all of the conclusions of the above-mentioned investigators are yet proved, due to various details of the technique employed in the experiments, and of laboratory conditions involved.

conditions in all of the crabs which were known to be courting. Two of the most striking illustrations will be summarized here and are typical of the rest.

Only adult males and females of *stylifera* were found on the relatively firm muddy sand shore above the mud flats at La Boca. They occurred there in increasing numbers throughout February, and it seemed likely that they migrated from the soft, damp flats to court on the dryer ground. (*U. saltitanta* and others, however, manage to keep clean and carry on a strenuous display in the midst of the mud-flats.) Courting males of *stylifera*, after emergence in the morning, changed from dull gray with the major cheliped chiefly brownish or yellowish, to pure white with the major cheliped orange, yellow, pink and white and the ambulatories bright purple. There was a brief intermediate phase where the carapace was brilliant yellow instead of white. It appeared that for the first one to three days an individual male was on the beach, and before he was displaying fully, the carapace brightened daily only to this yellow phase.

A male *stylifera* which coaxed a female, after prolonged courtship, to follow him down his hole, promptly enlarged it, then stopped it up with both of them inside, and remained with her there until the following low tide. The next day the male was in poor coloration and did not display. The female had vanished.

The courtship of a male of this species with the major cheliped in process of regeneration and only half size was observed throughout three weeks. Although otherwise normally colored—with dazzling white carapace and the legs purple—the regenerated member changed daily from drab gray brown to perfectly white, like the carapace, instead of yellow, orange and pink. This individual courted two females impartially for days until one moved away; he then paid all his attention to the other; I never saw copulation take place, nor saw either female attracted to his hole, but both often allowed him to approach and stroke them at the edges of their holes. I never, however, saw them stroke him in return, as in a consummated courtship between a normal male and female. For further details concerning this species, see p. 171.

The other most striking example of color change occurred in *latimanus*. The females, young and non-courting males, no matter how large, as well as males newly emerged from their holes after high tide, were similarly colored, the carapace being brown with gold spots and the ambulatories brown banded with dark; in the case of the males the large cheliped was dull chestnut brown. In these crabs it was a stricter rule than in any other species that only displaying males changed color daily, and conversely that all males which changed color displayed; finally, all of these and only these, built shelters (see p. 157). In the displaying males, the carapace each day, after feeding, during shelter building, and before display started, became pure white, the major cheliped chiefly bright orange, and the anterior sides of the ambulatory meri plum red.

In this species the display-color-change-building cycle was definitely under tidal influence. When first observed, on the last three days of January and the first two of February, during the spring tides of new moon, practically all the males high on the beach, with holes covered with water only during the highest tides, were displaying, while none of those lower down were doing anything save feeding and repairing their holes. Among this latter group not so much as a single waving movement was seen, although full grown males were as numerous as near the high water line. Similarly, in contrast to the upper group, males and females paid no attention to each other and I did not see a single fight go beyond the stage where the owner of a hole moved menacingly toward a trespasser, his cheliped thrust forward, *without waving;* in each of these few cases the threatened crab moved off promptly. In the following days of neap tides, when the water did not reach the upper part of the beach, the members of the upper colony remained in their burrows, six inches to a foot underground, for eight days (February 3–11). When dug up they appeared to be in a partial coma, and did not try to escape for half an hour or more. During the succeeding spring tides of full moon these upper colony crabs reëmerged, repaired their burrows and fed, but only a single individual on a single day displayed, changed color and built a shelter during the entire period. They again remained in their burrows during neap tide, reëmerging during new moon around February 25. Again there was no display. On the lower part of the beach, at this new moon period, however, a wave of display, color change, shelter building, mutual interest between the sexes and duelling, swept over the colony, exactly as it had four weeks previously higher on the beach. Observation unfortunately had to stop while this second courting wave was at its height. No actual copulations were seen, but several times females were observed to follow males down their holes, after watching long displays, and many more abortive courtships were observed, in which the female lost interest and moved away. (See also p. 157.)

In both these species, *stylifera* and *latimanus*, as well as in the others which changed less spectacularly, the display coloration was swiftly lost when the crabs were captured. The time required daily for the assumption of courtship coloration varied in different individuals and, to a lesser extent, in the same individuals on different days. One of the swiftest to change after emergence in the morning was *stylifera* which, on brilliant days, became fully colored within 15 minutes or less; one of the slowest was *latimanus*, which sometimes required two hours or more. The slowness is probably explained by the fact that *latimanus* always built a shelter before displaying, which necessitated its coming in contact with the damp sand and, apparently, dryness and sunlight are almost equally important in effecting color change; however, no experiments have as yet been conducted on this subject. Females, young, and non-courting males also brighten somewhat after emergence, but the

brightening consists only of emphasis of the prevailing drab colors, and is probably due as much to drying off as to exposure to light.

One of the most interesting aspects of display is the fact that ten of the twelve species studied show brilliant colors on the anterior side of the merus of the first three pairs of ambulatories, areas which can be seen only when the chelipeds are widespread in display. Another point has already been mentioned, namely, that in *beebei*, a relatively dull-colored form, almost the brightest portion is its iridescent green carapace: this species alone was observed to revolve in front of the female before which it was displaying; it is noteworthy that the ambulatory meri were as brilliant posteriorly as anteriorly.

The display coloration of the males of various species as far as known may be simplified and summarized in the following table. For the species in each group refer to pp. 165ff.

| *Courtship Color* | *Group 1* | *Group 4* | *Group 5* |
|---|---|---|---|
| Carapace | Gray or white | Purple, brown-and-white or white | a. Iridescent green, or iridescent blue and white<br>b. Gray or white |
| Cheliped | Purple, orange, yellow and white in each | Purple-and-blue, brown-and-white, or white | a. Purple-and ochre or pink-and-white<br>b. Each many shaded, orange through magenta |
| Ambulatories | Gray or purple | Purple-and-blue, brown-and-white or white | a. Gray or red<br>b. Gray or white |
| Anterior side of ambulatory meri | Major side salmon orange, minor side white | Peacock blue, purple, pinkish, white | a. Purple-and white, or scarlet<br>b. Yellowish, plum red, white |
| Buccal & pterygostomian regions | White | Turquoise, brown, white | a. Green-brown, white<br>b. Blue-and-green or white |

Group 1 is, in regard to color as in physical form, the most homogeneous; the other two vary considerably in the different species. No group is characterized by colors specially confined to them. One of the most outstanding traits of coloration is the prevalence of white carapaces, which are found in all three groups, in a total of six species, although one of these six has the anterior portion bright blue. Often these species go through a phase of bright or dull yellow, or of ochre-streaks, before assuming the pure white. The phase before the yellow is usually dull gray. The gray carapaces found in *princeps* and *deichmanni*, the close relations of which display in white, may be evidence of relatively low development of color in these two species, corresponding to their relative lack of specialization within their respective groups. Possibly, however, none of the numerous specimens observed displaying was in full coloration: the examples of *princeps* were all small, around 15 mm. in length, although they acted in every way like adults.

In the twelve species studied it is interesting that the most highly specialized forms in each group—e. g. *stylifera, saltitanta, stenodactyla, latimanus* and *terpsichores*—have the most arresting coloration, in which dazzling white plays an important part: in all except *stenodactyla*, which is brilliant blue in front, white or pinkish-white behind, the carapace is completely white, *terpsichores* is white except for the cheliped, and *saltitanta* is altogether white. (It is in the two latter species alone that the anterior ambulatory meri are not specially colored.) In all of the above species, too, the displays are more highly organized.

*Copulation:* Actual copulation was observed in *stylifera, beebei* and *stenodactyla*, a total of five times. In each case it was similar, taking place at the mouth of the female's hole after a more or less prolonged and intense display which sometimes, apparently, lasted for days between the same two individuals, subject to innumerable interruptions by the hesitation and frequent withdrawal of the females as much as by alarms from birds. Each copulation witnessed was preceded by mutual stroking of the legs and carapace with the ambulatories. The position was exactly similar to that illustrated by Pearse (1914.1) for *pugilator* in the laboratory. The two crabs faced each other, sternum to sternum, abdomens bent back, that of the male inside that of the female, the anterior ambulatories of each grasping each other around the body, the female with her posterior three pairs on the ground, supporting most of the weight of both. The chelipeds of the male rested above the female, the minor lying lightly on her carapace behind, or sometimes on top of, her eye, the major always clearing carapace and eyes, held flexed and perfectly quiet. The two remained together, quivering at first then quiet, for a very short time, up to three minutes; then the female would very gently disengage herself and slip down her hole, which she soon closed up, regardless of the position of the tide. In at least one instance, the male definitely stood guard over it afterward and warned off other males, *without* waving the cheliped rhythmically.

In *heteropleura, stylifera, saltitanta, beebei, stenodactyla, latimanus* and *terpsichores*, females

were seen to follow males, after vigorous display, down the holes of the males, remaining for anywhere from a few seconds to at least until the next low tide, since they did not emerge before the tide covered the holes. Always, during courtship, the male appeared to employ inexhaustible patience and gentleness except in two cases involving *princeps*, when two males of this species, on different dates, displayed briefly, then crept up on indifferent females from behind and tried, unsuccessfully, to drag them over to their (the males') holes.

It is probable that copulation usually takes place in the burrow of the male, but that when the female has been brought to the proper pitch of excitement at the mouth of her own hole, copulation takes place there, since her burrow is usually too small in diameter to receive the male. Provision for safety from birds and lack of interruption would seem to encourage copulation in the hole of the male, but the difficulty experienced by the males in arousing the females would explain the occasional surface pairings.

Pearse's observation that copulating females are hard-shelled was supported by my own observations. For further details of pairing, see below and pp. 173, 193, 196.

*Shelter Building:* In 1873 Verrill reported that specimens of *minax* built "ovens" above their holes. Matthews, working in Brazil on *leptodactyla*, made a similar observation. He described the method of building very accurately, his observations checking with my own made in Panama on *beebei*, *latimanus* and *terpsichores*. He attributed to the "hoods," however, the function of keeping the burrows from drying out in the hot sun. Whatever their function—which I have not yet discovered—it cannot be this, for it is *only* courting males that build shelters; the shorter burrows of the smaller females and young surely need protection far more than those of large males, yet this device is never used by them; instead, when the sun becomes too hot for them they use a simple plug to close their burrows, or push up material from below.

Of the three Pacific forms which were seen to build shelters, the instinct is least developed in *beebei*, best in *terpsichores*. In the first case the form of the shelters varies from little more than a pillar of sand beside the hole to a fairly well arched hood, little higher than the builder; also, it is not built by all displaying males, and is not necessary to win a female, since in the case of one of the two copulations witnessed in this species, the male had no shelter; in the other there was a well built shelter which played no apparent part in courtship. In *latimanus* a well formed shelter is always built by every displaying male. In *terpsichores* on the other hand the shelter is the best formed of all, and relatively the largest, but it is not built by every displaying male; however, the breeding season was waxing in this species when I left, and increasing numbers of shelters were being built every day. Incidentally, *terpsichores* and *latimanus* are closely related, and *beebei* more distantly, but all belong to the same group of highly specialized crabs, all of which are adapted for life on relatively firm, dry ground. Only *beebei* occurs on mud-flats as well as on muddy-sand beaches; in the mud-living individuals, the building of shelters is more spasmodic and unsuccessful than ever; the very nature of the semi-liquid mud would make the erection of a well-arched shelter almost an impossibility.

This mysterious habit of building is probably a special development of the practice of stopping up the hole with a plug before the tide covers it. (Incidentally, this latter practice in the Pacific species studied is very casual, being rather frequently omitted by individuals in each species without any apparent reason). In making the shelter, as in plugging up the hole, the legs of the major side are used in scraping up and carrying the sand, and patting it into place, the crab always working from the underside of the growing half-dome. This method is in direct contrast to that employed in hole digging, when the minor side is invariably employed. It would seem that there is a distinct waste of effort when the crab, as often happens, first repairs his burrow, dumping the loads of sand several inches from the hole, and then builds the shelter, scraping the sand from a similar distance, but never using excavated, already loosened, damp sand for this purpose. The separate origin of the two activities explains this lack of correlation. For further details on the building activities of the several species see pp. 194, 203. On p. 196 is an account of equally inexplicable wall-building in mature females of *stenodactyla*.

*Behavior of Females during Courtship:* As has been said, the role of the female, until the final stages of courtship, is one of complete indifference or definite retreat. Each male must display for long periods daily in the hope of attracting the attention of a single female sufficiently to make her pause in eating or passing, and watch him. Once this is accomplished, courtship may proceed a dozen times a day to the point where copulation is about to take place, only to have the approach of a bird, or, even more frequently, the recurrent withdrawal of the female—often accompanied by the abnormally early plugging of her hole for the day—interrupt the courtship. The latter is resumed only after a repetition of lengthy preliminaries. In the cases observed where females either followed males down their holes, or mated with them on the surface, the successful male was sometimes only moderately large and brightly colored, compared with the most spectacular in size and color of the same species.

How females, all so similarly formed and inconspicuously colored, are recognized by males of their own species in mixed and crowded colonies remains a major mystery. Beebe observed a phenomenon in *mordax* which was also frequently apparent in various species in Panama, namely that a particular female often had the power to stimulate any number of males to violent display, merely by ceasing for an instant

to feed, or by emerging from her hole, or wandering a few inches from her usual position, whereas other individuals, equally large and of identical coloration, attracted little or no attention from the same males at the same time. For the behavior of *stenodactyla* when pursued by males, see p. 196.

*Origin of Display and Comparison:* Little work has been done on courtship and mating in other groups of crabs. The principal study is that by Chidester (1911), who found that sex discrimination is tactual in *Callinectes*, *Cancer*, *Carcinus* and *Platyonychus*. In *Uca* it is certainly not tactual, but instead largely or completely visual. As in Chidester's examples, however, once a female has permitted a male to touch her—except in the case of females pursued and encircled by male *stenodactyla*—the female is not passive in the movements preceding copulation.

Hediger (1934), although he does not think that waving of the large cheliped has anything to do with courtship, nevertheless presents a most sensible theory of its origin: "It is clear that the lifting of the chelae originated as a preparatory fighting motion (compare with other crabs), which as in many other cases, became only a threatening gesture, then was developed and transformed in this group into the signalling motion."

From my own observations, it appears that waving may be carried on throughout the year by many species of fiddlers, especially, perhaps, by the less highly specialized forms, as a purely threatening gesture, warning encroaching crabs away from a chosen feeding ground surrounding the hole. This type of display is relatively phlegmatic—unless an actual fight is imminent—and is often carried on with a perfunctory air while the minor cheliped is engaged in feeding. During the breeding season, however, the tempo of waving is greatly accelerated, and the activity is now devoted chiefly to the end of attracting females. Slow-waving-*cum*-feeding periods still occur at this time, a habit which obviously enables a crab to advertise himself to females which might pass him unnoticing, if he did not wave while he ate. The function of waving in warning off males at this time also seems definitely connected with courtship in most cases, since the females in a given territory are perhaps more or less consciously preëmpted by the male. At least during the breeding season, when most of my observations were made, no male was ever seen to attack any except adult or nearly adult males; females and young came and went as they pleased, and there was far greater toleration between males of different species than between those of the same kind. Also, in a number of forms—especially in *stenodactyla*—females have been seen very definitely to be the cause of duels between males.

The conclusions of Verwey and Hediger, that waving has nothing to do with courtship, may be explained by the fact that courtship display may prove to be poorly developed in *signata* and *tangeri*, while their property sense is strong. On the other hand, it may be that neither of these observers witnessed actual courtships in mid-breeding season. The latter explanation is perfectly possible, even though Verwey, at least, must have spent a great deal of time in observation: in Panama I had to wait days to see proof in certain species that males were actually stimulated to energetic display by interested or potentially interested females, and that the females without question paid attention and were influenced to receptivity by the display activities, marked by waving, of the males.

In other sections of the animal kingdom, notably among birds, a number of cases are known where the courtship display or behavior is scarcely different from, or is identical with, warning and threat. Among the best known are the displays of pheasants, grouse, and certain sandpipers and other wading birds. The same is true of many songs: the male sings both to attract the female and to let possible rivals know, preferably without a fight, that he is in possession of a nesting site and will challenge interlopers.

It is interesting to remember here that where, in the lyrebird and bowerbird the display has outgrown its function as a specialized part of the mating cycle and, as has been suggested, perhaps "become very largely of an almost recreational nature" (Stoner, 1940, p. 98), carried on throughout the year, the opposite seems to have happened in the case of fiddler crabs, where courtship display probably arose from year-round threat activities. In *latimanus*, at least, it seems now to be restricted to the breeding season.

The marvelous correlation between display and color found in the various species of birds of paradise is found to a lesser extent, but no less unquestionably, in fiddler crabs. Since courtship dances are well known in a number of insects and spiders, there seems to be no reason to deny the existence of such displays among crabs on the basis of their being invertebrates.

*Conclusions:* From the foregoing data on *Uca*, a few conclusions may be drawn concerning the functions of display which are applicable to the species studied at Panama, all of which appear to be relatively highly specialized forms. It is important to remember that these conclusions are not necessarily true of the entire genus.

1. Waving and its accompanying behavior in fiddler crabs form, in the various species, distinctive displays which are complemented and supplemented by temporary coloration patterns. These colors are shown to the best advantage only when the crab is in the midst of display.

2. No evidence at all has been found of the influence of sexual selection in the old-fashioned sense—that is, of a female's deliberately choosing a brightly colored or especially active crab for a mate in preference to one which was duller or slower. Nevertheless, display coloration is so closely linked with the characteristic display in the various species, that it seems very unlikely that coloration is only an accidental and useless result, or a mere waste product, of glandular

or other physiological activity, or that display is simply the result of excess energy. Instead, it seems certain that females do distinguish and recognize males of their own kind by both motion and color—as well, perhaps, as by scent or some other means—and that they are eventually attracted and stimulated to mate by the display of persistent males, which are usually among the most brilliant or acrobatic.

3. At the same time, display doubtless serves also as a warning to rival males to keep away from a chosen feeding and display territory surrounding the hole. This function also is performed in other seasons of the year in some, but not in all, species.

4. Associated with display in certain species is the erection of shelters of muddy sand above the hole. No function can be attributed to these yet, except that they probably serve as further advertisement of the presence of a male in breeding condition.

### G. Breeding and Growth.

The observations at Panama were all made between January and March; the ovigerous females in the *Zaca* collection from the west coast of Central America were also taken at this season, but since these dates coincided with the dates of both trips, no real conclusions can be drawn. However, since sunlight and dryness are needed to bring out the display colors of males, and since these months are the height of the dry season, it seems reasonable to assume that fiddlers have at least a major breeding season at that time. Evidences of sexual rhythms were seen in the species studied, some being apparently near the close of the breeding season while others were obviously entering it. Some (e. g., *panamensis* and *umbratila*) were not displaying, except for a few abortive displays in the former species, nor were ovigerous females seen. An account of tidal rhythm in the display of *latimanus* has already been given (p. 155).

Ovigerous females appeared to move around less than non-ovigerous ones, but were frequently seen feeding in full sunlight. They were never the object of display by a male. It seems likely that ovigerous females of the *stylifera* group, at least, come ashore to copulate, but go down to the mud flats to carry their eggs (p. 172). No fiddlers were seen at night, even in full moonlight, on the two evenings when observations were made (c. f. Pearse, 1912).

The eggs, counted in eleven species, numbered between 500 and 15,000, relatively low totals compared with those of cancroid crabs, for example. Similarly, the eggs are relatively larger, and of remarkably similar sizes, ranging between .24 and .27 mm. in diameter.

No special studies have been made on development, but from time to time in the following pages notes are included on the general growth trends and characteristics of young crabs of various species, which will be useful only in identification and as hints on intrageneric relationships. Detailed work must wait for the future.

Apparently no holes are dug until at least several crab instars have been passed, and the crab reached a length of 3 mm. or more. Before this time the crabs run freely in and out of the burrows of larger crabs of both their own and other species.

Young crabs in their physical characteristics, as is to be expected, frequently give clues to their relation to other species. For example, the young of *macrodactyla* can with difficulty be distinguished from adults of *zacae*. As is well known, the young lack the characteristic ridges inside the palm, the whole cheliped gains its size and elongate chelae only gradually, and often the orbits are more oblique than in the adult. Often, too, there is more pile on the carapace, or pile which is quite absent in the adult (as in *umbratila* and *oerstedi*). In *stenodactyla*, *latimanus* and their allies, however, with the carapaces semicylindrical and the orbits scarcely oblique, the orbits even of crabs less than 2 mm. long are similarly almost straight, although the carapace is relatively flat. In the young of crabs of the very narrow-fronted group containing *princeps* and allies, the front is wider than in the adult, but still so narrow that there is no danger of confusion with other groups of species. Spoon-tipped hairs on the second maxillipeds are fewer in young than in adults (see p. 161).

*Precocity:* Adolescent males, distinguishable by their smaller size and short-fingered chelipeds, sometimes may be observed apparently in the midst of learning to court and build shelters. These individuals have not attained full courtship coloration, and their movements during display show various stages of practice. The display usually is erratic and casual. Similarly, shelters may be started but not completed, or the crab may spend an entire morning building a structure which is small and badly made. Once I saw such a shelter toppled over by a strong gust of wind.

Special examples of precocious behavior were noticed in *beebei*, where an obviously immature male, without a shelter and in poor coloration, induced a female to follow him down his hole, after an energetic display. Once she was down there, however, he became frantically restless and popped out and in again every few minutes, displaying vigorously in the direction of other passing females. Another young male, this time a *stenodactyla*, after fruitlessly courting a female who paid no attention whatever, and who finally vanished down her hole around which she had just finished building a high wall (see p. 196), deliberately walked over to her wall and pulled it down with his ambulatories, trampling it into the ground until no sign of it was left. He then returned to normal feeding, without display, beside his own hole.

### H. Individuality and Play.

A strong spirit of individuality was observed in the fiddler crabs, and I agree with Pearse (1912,

1914. 2) that some of their behavior can only be interpreted as sheer play. Several adjacent males of similar size, belonging to the same species, on the same day would show definite traits of individuality. One would be especially belligerent, seeking every excuse for a duel; another would build a shelter and display strenuously all day, scarcely stopping to feed; the third, although he had spent most of the preceding day fighting and courting, might on this morning feed continuously and enlarge his burrow, punctuating this activity with only a few half-hearted displays.

Similarly, some females of various species were much given to wandering about, peering down the holes of adult males, hurriedly retreating, paying brief and successive attention to the displays of a number of neighboring males, and altogether behaving in a manner which in higher animals would certainly be termed coy and flirtatious. I have used these ultra-anthropomorphic terms advisedly, because I have been unable to find any other words in the language which so exactly define the actions of these individual females. Others, of the same species, spent hours feeding quietly on several square inches of ground. In the end members of the latter group proved just as susceptible as the wandering individuals to the advances of displaying males.

Two large male *stylifera* furnished a good example of a social relationship of sorts which continued for at least a week. Their burrows were a yard apart, in an uncrowded portion of the beach, although other males of their own species were close by. Every day they followed an invariable routine, consisting of emergence, cleaning, feeding, accompanied by change to display coloration, and then—without a sign of preliminary waving or warning or argument of any kind—they would meet on the invisible boundary line between their burrows and fight. The duel always ended several minutes later in identical fashion, the smaller being somersaulted backward by the larger. The vanquished would then pick himself up and retreat hastily to his burrow, while the winner resumed feeding without another glance. After a half hour or so more both would begin to display, without taking any further notice of each other. I never saw two fights in one day, and there was never any female in their vicinity. Finally both moved away and I lost track of them.

The apparently sporting aspect of part of the courtship activities of *stenodactyla* is described on p. 196.

One of the most individualistic, inexplicable performances I saw was that of a moderate-sized but apparently adult male *terpsichores*. His display coloration was not well developed on the day in question, his usually white carapace being heavily streaked with dull yellow and his cheliped scarcely pink. He did not build a hood or display, but enlarged his burrow and fed energetically. Then, suddenly, he went straight over to the newly erected shelter of a neighbor fully eighteen inches away. Without any provocation or preliminaries he undermined the shelter from the rear and pushed it down on top of its owner; the two crabs then spent 15 minutes fighting, in the course of which both darkened rapidly, losing all trace of display coloration, and the shelter owner lost the tip of his pollex. Finally, the aggressor let the owner go, then went directly to the next hood, six inches from the first, and repeated the episode exactly. In this case, too, the owner was powerless and was constantly thrust down his own hole, although he put up a good fight. At last, after another 25 minutes of uninterrupted struggle, the aggressor released this crab also, and returned, without any hesitation, to his first victim, who by now was cleaning himself up and had regained most of his display coloration. At the approach of his former antagonist, the victim tried to flee down his hole, but was seized from behind. Another duel, lasting no more than several minutes this time, followed, and ended as on the first two occasions by the aggressor's abruptly releasing his victim. This time the former returned slowly but directly to his own hole, cleaned himself, and began to feed. Neither of the two victims rebuilt their shelters on that day, although the tide was only slightly past dead low at the time.

The general conclusion to be drawn from all this variability of action is that fiddler crabs, nervously the most highly organized of all crustacea, show a truly remarkable latitude of behavior. This is especially striking when fiddlers are compared with ants and bees, which are tied down to severely patterned behavior by the hyper-development of their social organization.

## I. Enemies and Defense.

Along the coast of Central America the greatest enemies of fiddler crabs are shore birds. At La Boca alone five species of herons, snowy and American egrets, curlews, sandpipers, herring gulls and great-tailed grackles hunted fiddlers daily at low tide. At Port Parker, Costa Rica, numerous sandpipers were hunting them. Everywhere, too, raccoon tracks were found among the fiddler holes, especially on mornings when the low tide came very early. Fiddlers were also taken from the stomach of a lizard, *Ctenosaura similis*, at Culebra, C. R., and from that of another, *Basiliscus galeritus*, on Gorgona Island, Colombia.

The crabs are adept at escaping all these enemies, and yet in wasting as little time under cover as possible. Each colony, whether mixed or formed of a single species, has worked out a scale of alarms based on the movement of suspicious objects. At La Boca noises, ranging from the cries of their bird enemies to the shouts of human beings, whistles, cannon-fire and dynamite, had no meaning for them. Neither did the passing of butterflies and wind-blown leaves within an inch or two of their eyes. But a bird flying over within twenty-five feet or a plane within, say, two hundred, was the "alert" which sent all the crabs scurrying to the mouths of

their holes, where they froze, poised for instant flight within. The "take cover" signal was the approach of a bird either on foot or wing within ten to twenty feet, depending on both bird and crab, and the approach of a human being within, on the average, thirty feet.

This distinction among "no cause for alarm," "on the alert," and "take cover" must save them a great deal of time for feeding and courting during every low tide. A most interesting point is that brightly colored adult males are the first to enter their burrows and the last to leave.

## V. Phylogeny.

The study of the present collection of eastern Pacific fiddler crabs has shown the importance of a number of physical characteristics to which little attention has previously been paid. These, combined with the occurrence of eleven species hitherto undescribed, have clarified considerably the relations of the various species to one another. In spite of the fact that no complete picture can be formed until the genus as a whole has been similarly and more exhaustively studied, it seems worthwhile to present some tentative conclusions in regard to these relationships. (Text-figure 5).

The first necessity was to discover the primitive forms of the various physical characters, in order to decide which species were as a whole the least specialized. It appears that in a theoretical, primitive *Uca* the carapace is moderately arched, strongly narrowed behind, the orbits strongly oblique, the front moderately narrow, the major cheliped relatively small with short fingers and lacking tuberculated ridges across the palm, the minor cheliped with well developed teeth and a slight gape, the third maxilliped with a rudimentary median groove traceable only anteriorly, the second maxilliped with a moderate number of spoon-tipped hairs, and the abdominal appendage stout with a thick arm near its tip. It would presumably live in a fairly stable environment, not subject periodically to great dryness, and would have neither coloration nor display highly developed. A few species, especially *pygmaea*, *argillicola* and *helleri*, fulfill the majority of these conditions, although each of these three has already started to specialize in various divergent fashions. Unfortunately, the display of none of these has been observed.

From this theoretically primitive form, specialization has proceeded in a number of directions. These may be divided into ecological and structural, the latter being closely dependent on the former. For this reason, the former will be listed first.

### 1. *Ecological Specialization.*

a. Moving from stable, damp habitat, such as briefly exposed mud-flats, or mangrove marshes, to a periodically dry habitat, such as sloping shores or the banks of small fresh water streams.

b. Color change associated with courting.

c. Shelter-building associated with courting.

d. Display dances associated with courting.

From available material, it appears that b, c and d are most highly developed in those crabs which have been most modified for a truly littoral life.

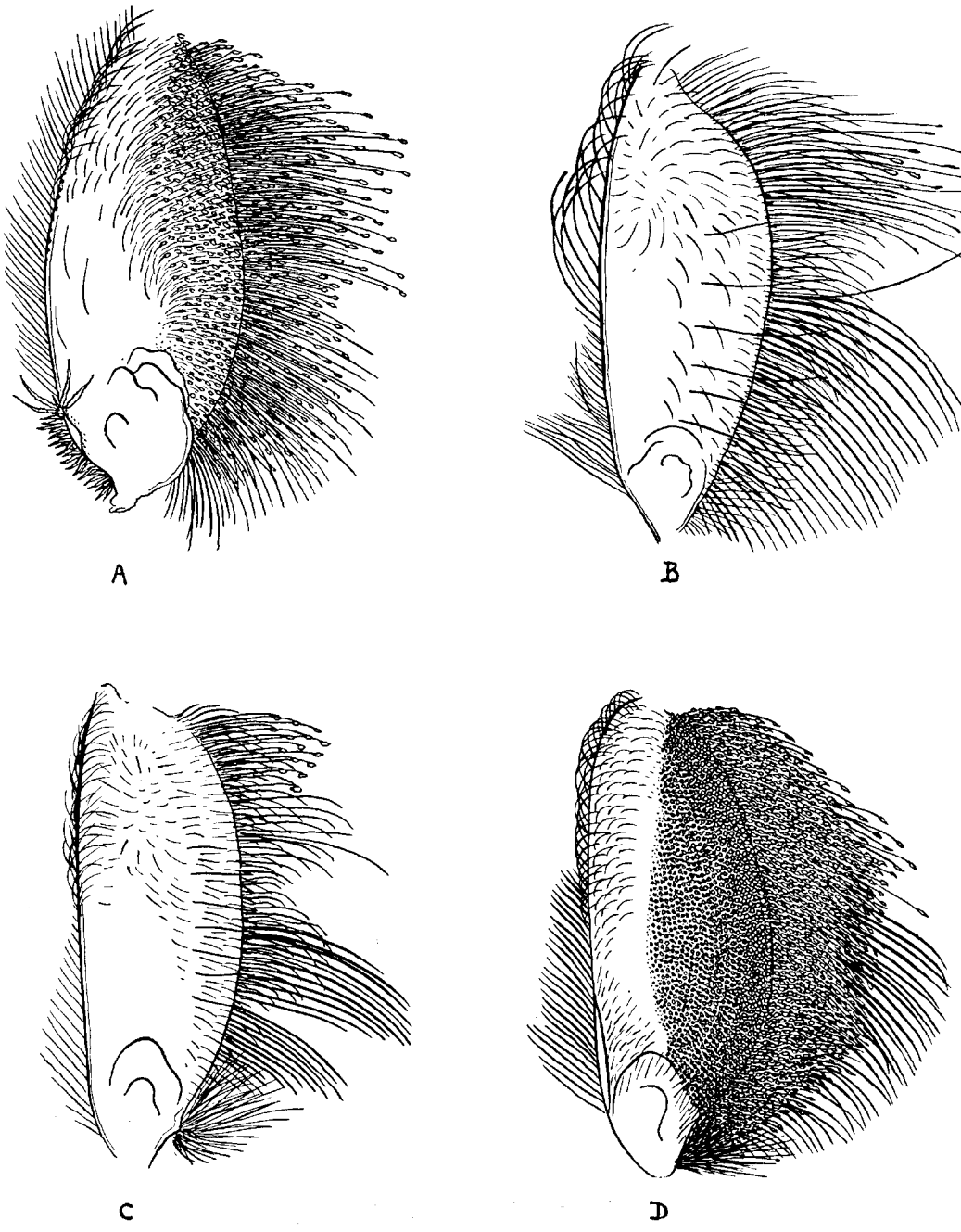
### 2. *Structural Specializations.*

a. *Increase in Thickness, through Great Arching of Carapace and Underparts, Straightening of the Orbits, Divergence of Carapace Sides Posteriorly, Fusion of Abdominal Segments:* These modifications serve the two-fold purpose of guarding against dessication, and of giving more room in the branchial chambers for the exposure of blood-vessels, an arrangement which functions as a primitive lung when the crab remains out of water for so long that the gills become temporarily useless. This increase in thickness, accomplished by most or all of the means listed above, becomes evident in end-species of Groups 2, 4 and 5, forming a good example of convergent evolution. It is most highly developed in Group 5, in which the end-forms all live a strictly littoral existence and spend hours daily exposed to the sun and air. The bottoms of the burrows of *latimanus*, the thickest of all, may not be covered by the tide for more than a week at a time. Although the species in Group 1, characterized chiefly by very narrow fronts, are in an isolated series, they are in many particulars highly specialized. They are all fairly flat, and there is some evidence to show that they come ashore only to court, but otherwise live on briefly exposed mud-flats. *U. panamensis*, the specialized crab forming Group 6, is noticeably flattened; this is probably associated with its unfiddler-like habit of hiding under stones.

b. *Specializations of Mouthparts:* The significance of most of these adaptations cannot even be guessed at. They include:

i. Grooving or smoothing of ischium of third maxilliped (Pl. VII). In the least specialized forms, and continuing through all groups except 2, 3 and end-species in Group 5, the ischium is moderately flat with a well developed inner groove and a central groove represented only by an anterior (distal) median depression. In the end-forms of Group 2 the median groove is progressively better developed, extending posteriorly (basally) and swerving inward to fuse almost or completely with the basal end of the inner groove. There seems to be no practical significance to this trend, except to show a fundamental relationship. In Groups 5 and 6 the ischium is practically smooth except for an inner groove, being flattened in Group 6, as is the rest of the crab, and broad and swollen in Group 5, the swelling being obviously merely a continuation of the general tendency to increase bulk in order to mitigate dryness.

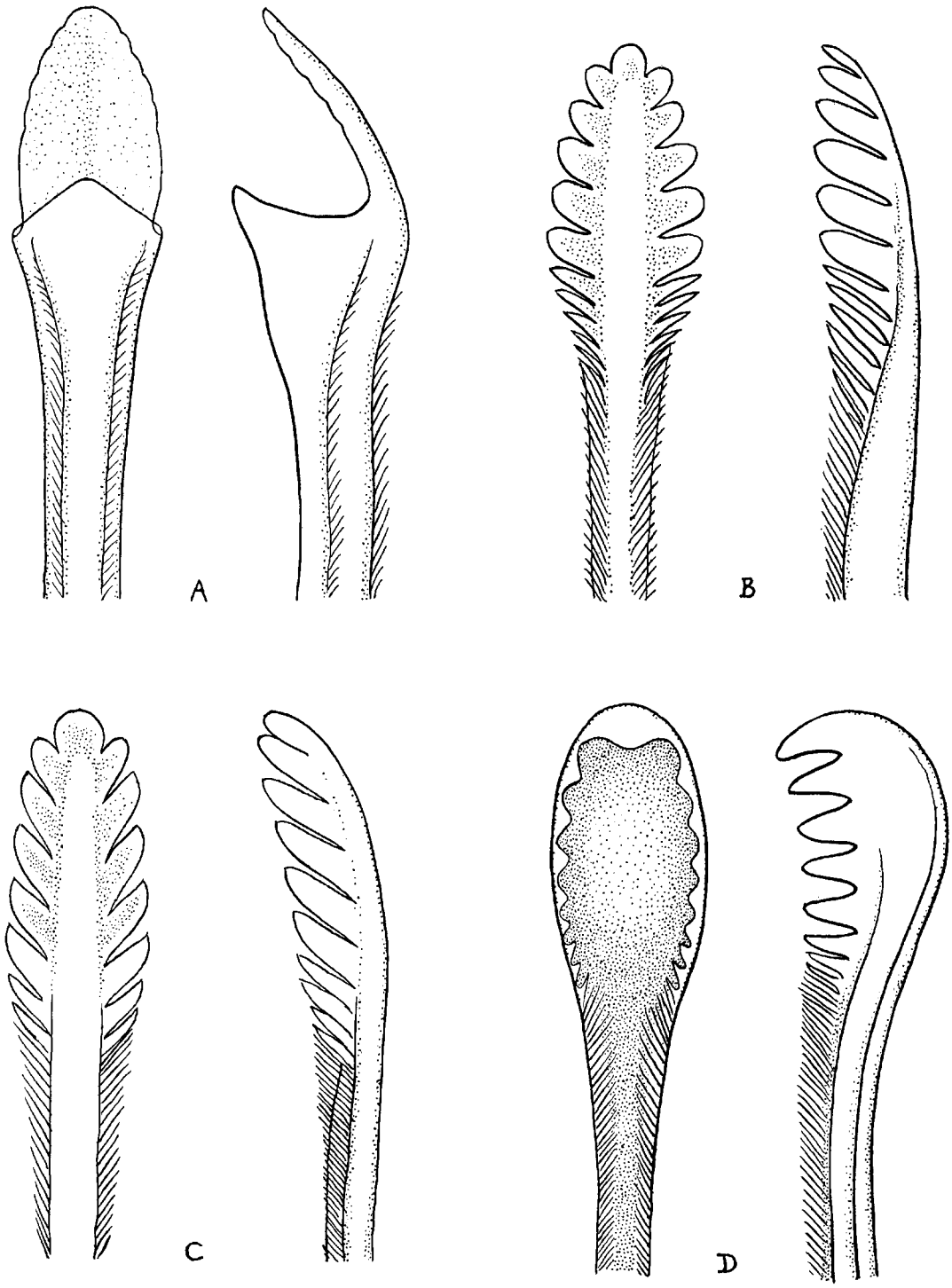
ii. "Spooning" of hairs on merus of second maxilliped (Text-figs. 2, 3). The most usual state is for the inner edge of the anterior half of the merus and the tip of the palp to have many or all of the hairs terminating in concave, pectinated




Text-figure 2.

Inner (dorsal) view of merus of second maxilliped in *Uca*. **A**, *princeps;* **B**, *mordax;* **C**, *oerstedi;* **D**, *latimanus*.

expansions, termed "spoon-shaped" for the sake of brevity. Departure from this norm extends in both directions, toward total reduction and toward tremendous increase, both of these departures taking place only in end-species. In Group 1 they are more than moderately numerous, and in addition have characteristic spines at the base of the shallow spoons, the pectinations of the latter being rudimentary. Throughout Group 5, where it reaches its highest development, spooning is further increased. On the other hand, in Groups 2 and 4 the spoons become progressively fewer, until in end-forms they are almost or completely lacking. Since they are best developed in species living at least part of their lives on muddy sand shores, as opposed to semi-

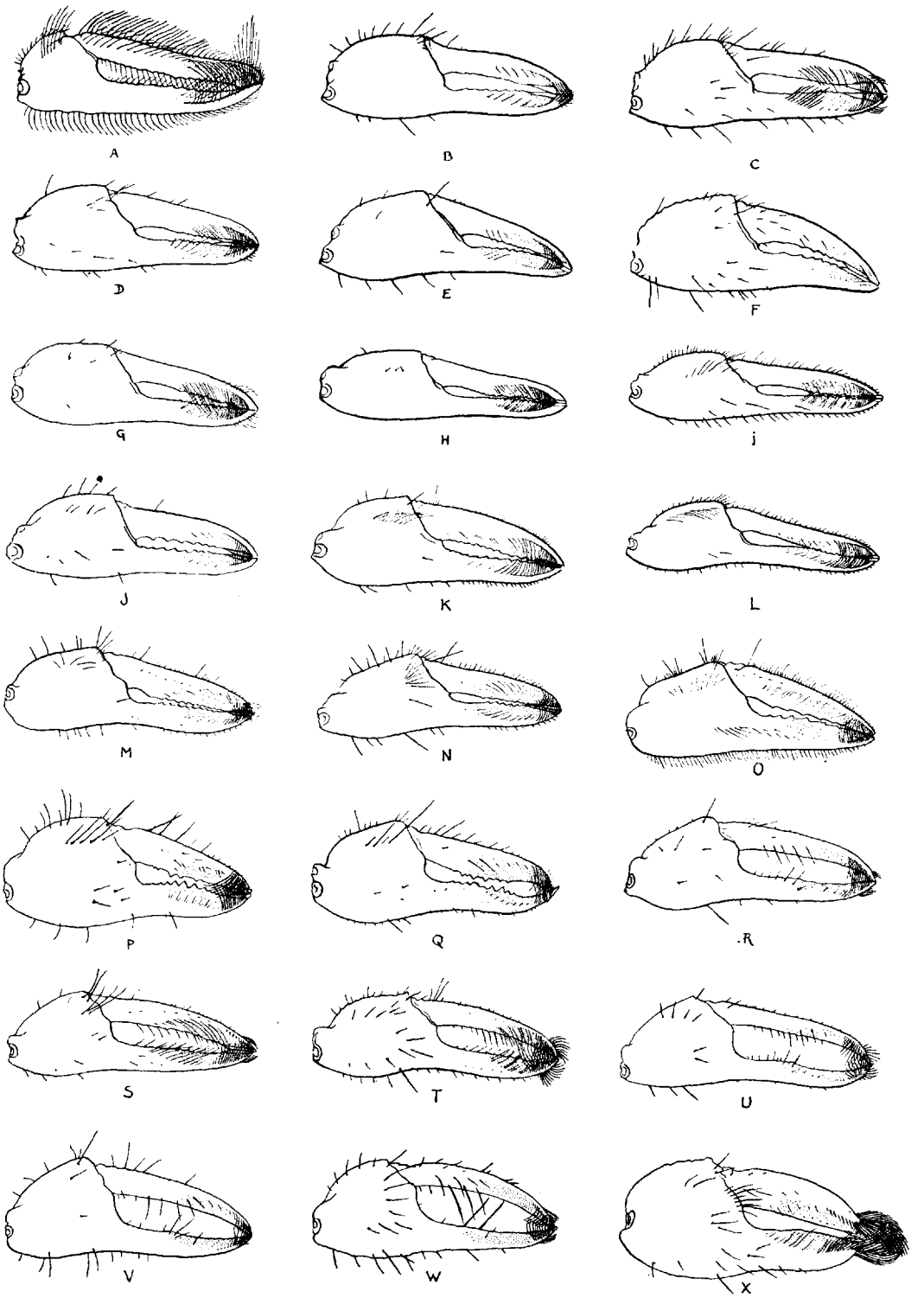



Text-figure 3.

Typical spoon-tipped hairs from merus of second maxilliped in *Uca*, front and lateral views. **A**, *princeps*; **B**, *mordax*; **C**, *oerstedi*; **D**, *latimanus*.

liquid mud, it is probable that their function is concerned with the sifting of organic detritus from this relatively dry medium.

iii. Development of "woolly" hairs on second maxillipeds. These structures have not been studied at all in detail, and they are included here




Text-figure 4.

Minor chelipeds in *Uca*. **A**, *heteropleura;* **B**, *pygmaea;* **C**, *zacae;* **D**, *galapagensis;* **E**, *mordax;* **F**, *brevifrons;* **G**, *macrodactyla;* **H**, *tomentosa;* **I**, *umbratila;* **J**, *argillicola;* **K**, *oerstedi;* **L**, *inaequalis;* **M**, *tenuipedis;* **N**, *batuenta;* **O**, *saltitanta* (♂); **P**, *beebei;* **Q**, *stenodactyla;* **R**, *helleri;* **S**, *crenulata;* **T**, *limicola;* **U**, *deichmanni;* **V**, *latimanus;* **W**, *terpsichores;* **X**, *panamensis.*

merely in order to call attention to their existence. The usual condition seems to be the occurrence of a moderate number of hairs clothed in a fuzzy material in a tuft on the inner edge of the ischium, and in a smaller tuft on the inferior (external) side of the tip of the palp. Usually there are also a few along the external edge of the merus. In Group 3 these structures are far more numerous than usual, and are somewhat increased also in Group 1. In Groups 4 and 5 they are progressively decreased, being very few in the end forms of both groups. It appears that they are most highly developed in those species living in the wettest mud, least in the truly littoral forms. The high degree of development of both spoon-tipped and woolly hairs in members of Group 1 is explained if sand-livers have more need of spoon-edged hairs in feeding, and mud-eaters of wool, since members of this species apparently spend part of their lives in both kinds of habitat. The mystery of how these specialized hairs are actually used remains, however, completely unsolved.

c. *Weakening and Loss of Minor Cheliped Teeth:* (Text-fig. 5): In Group 5, which contains the most littoral forms, the teeth progressively decrease in strength and finally vanish, this decrease being accompanied in an increase in gape and slenderness. The resultant weakness is compensated for by the strengthening of the terminal basket formed of interlocking bristles. The function of this adaptation, if any exists, is not clear. In *panamensis* (Group 6) these terminal bristles are enormously long, thick, strong and numerous, while the chelae are short and thick and toothless. These characteristics are almost certainly adaptations concerned with the crab's habit of scraping algae from the rocks.

d. *Variation of Form in the Major Cheliped:* This character is practically useless as an indication of true relationships. A number of species, very distantly related, and referable to various groups, have similar chelipeds, a general type having the fingers longer than the palm, with strong teeth, a moderate gape, and a well developed oblique tuberculated ridge on the inner side of the palm. In contrast, the two highly specialized and closely related end-forms in Group 5, *latimanus* and *terpsichores*, have utterly dissimilar chelipeds—short, broad and ridgeless, as in primitive forms, in the first species, and elongate, slender, and strongly ridged in the second. In Group 4, however, there is a general trend toward broadening and flattening of the pollex; it is possible that this is associated with the rapping of the ground in display, the increase in breadth giving perhaps more strength to withstand the rapping. However, in *batuenta*, one of the rappers, the pollex is scarcely broadened.

e. *Stridulating Ridges:* The first hints of stridulating mechanisms, consisting of a scattering of tubercles on the lower, basal, inner surface of the major palm which is opposable to a row of tubercles on the merus and carpus of the first major ambulatory, occur in *inaequalis*, a primitive representative of Group 4, and in progressively greater development through some of the species of Group 5. Unfortunately, no observations have yet been made on the use of stridulation in the field; it was not seen to play a part in display on the surface of the ground.

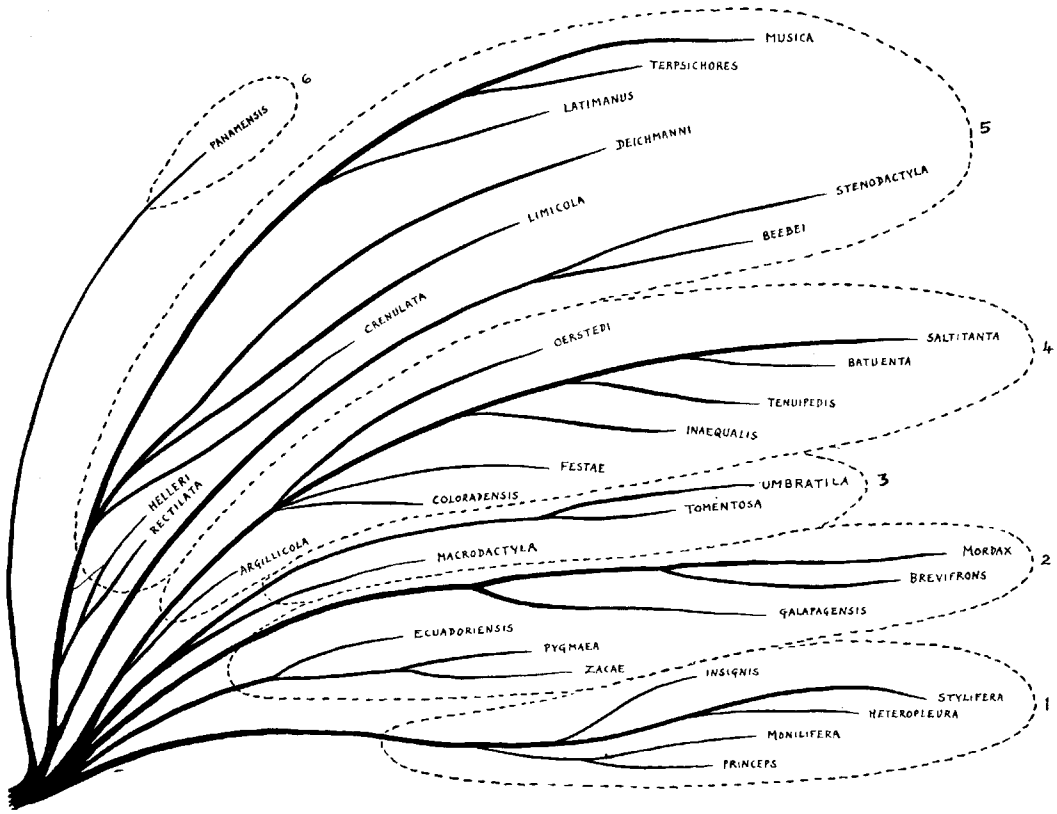
f. *Abdominal Appendage of Male:* The least specialized type seems to be short, thick, and blunt, with a short, blunt or spinous "arm" near its end. In Group 1 the end-species have slender appendages, with curved, tapering tips. In Groups 4 and 5 the appendage becomes progressively more slender and the arm reduced or absent in the end-forms of both groups. The pronounced curving of the appendage in the same species is apparently largely in conformity with the arching of the underparts in the provision for increased bulk. Some differences have been found in the form of the seminal receptacles of the females in various species. It would be interesting to work out in detail the specific adaptations of the male and female organs to each other.

g. *Color and Display:* Unfortunately color change and display have been observed only in Groups 1, 4 and 5, and until they are known in the other groups no trustworthy conclusions can be drawn concerning group relationships in this field. The prevalence of white in the display coloration of end-forms, the development of the rapping phase of display in Group 4, and the generally high level of display in all end-forms in the group have already been mentioned (p. 153ff.).

## Definition of Groups.

The characteristics of the various groups of west coast species of *Uca*, may, using the above data, be summarized as follows:

Group 1. *princeps, monilifera, heteropleura, stylifera, insignis.* This very distinct group, which perhaps should be a subgenus, is characterized throughout by having the front exceedingly narrow, carapace little arched, cheliped massive, the chelae broad and flat; spoon-tipped hairs numerous, covering from a quarter to a half of inner surface of merus, in many rows; the individual spooned hairs are very shallow and only slightly scalloped; at their base is a sharp angle sometimes projecting as a well-developed spine. The minor chelae are large, slender, the gape slight, articulating distally, with moderately strong serrations; all margins fringed with long, thickset hairs. The shape of the abdominal appendage in the male divides the group into two: in *princeps* and *monilfera* it is thick and blunt, with the anterior arm represented by a strong spine. In the other three it is slender, tapering, the arm terminal, projecting distally. In the first two there is a tubercle beside the seminal receptacle, in the last three there is none, and the receptacle is crescentic. Observed display coloration (not seen in *insignis* or *monilifera*) reaches its highest development in *stylifera*. All live on open tidal mud flats, and some at least come to adjacent muddy sand beaches to court.




Text-figure 5.

Tentative phylogeny of eastern Pacific species of *Uca*.

Group 2. *ecuadoriensis* (position based on type description only), *pygmaea, zacae, galapagensis, brevifrons, mordax*. These seem to be relatively primitive forms, living in shady, brackish or freshwater mud, in protected places. One branch has the orbits very oblique, and chelipeds characterized by the lack of an oblique ridge and rather short fingers. The other has well formed chelipeds, with ridges and long slender fingers. Their relationship is shown by the minor chelipeds, with weak or moderate teeth, a slight gape, and progressively fewer hairs, by the grooving of the third maxillipeds and the progressively reduced spooning on the hairs of the second maxilliped, and by the broad fronts. Display unknown.

Group 3. *macrodactyla, tomentosa, umbratila*. Members of this group live in mud among mangroves. The position of *macrodactyla* may be nearer to Group 2 than 3, since its front is very wide, whereas those of *tomentosa* and *umbratila* are notably narrow. However, in the form of the minor chelae, which are strongly serrated with little gape and plentiful hairs, in the medianly smooth merus of the third maxilliped, and in the generous number of spoon-tipped hairs on the second maxilliped, the three forms are very similar. Here again the trend is from oblique to horizontal orbits. Display unknown.

Group 4. *argillicola, coloradensis, festae, oerstedi, inaequalis, tenuipedis, batuenta, saltitanta*. In this group the trend is from the oblique orbits and moderately arched carapace of shade-living *argillicola* to the practically straight orbits and semi-cylindrical carapace of *saltitanta*, which lives on sun-baked open mud flats. Throughout the group the spoon-tipped hairs become progressively reduced in number until in the end-forms they are practically absent, the eyebrow becomes narrower, the crenulations on the lower orbital margins obsolescent, and the arm of the abdominal appendage reduced, obsolete in end-forms. In all forms the minor chelae are strongly serrated with a very narrow gape. The major pollex in a number of species is broad and triangular, especially in *saltitanta*. The display and display coloration of *inaequalis, batuenta* and *saltitanta* show an interesting progression involving lightening of the color to pure white and developing of the rapping phase of display.

Group 5. This group contains the most specialized crabs and is divided into two sub-divisions composed of *beebei* and *stenodactyla* on the one hand and, on the other, of *helleri, rectilata* (known from type description and Holmes, 1904, illustrations), *crenulata, limicola, deichmanni, latimanus, terpsichores* and *musica*. In all the carapace is strongly arched, completely semi-cylindri-

cal in all the end-forms, and the spoon-tipped hairs on the second maxilliped are enormously developed. In the semi-cylindrical species these hairs number hundreds, their bases covering most of the inner surface of the merus as well as projecting beyond the end. Throughout the series the eyebrows increase in breadth. In *beebei* and *stenodactyla* there are a few strong teeth on the minor chelae and the arm on the abdominal appendage is lacking; in all the others, however, the chelae are progressively almost or completely without serrations and widely gaping, and there is a well developed arm on the abdominal appendage. In all the end-forms except *latimanus* the major cheliped is large with long, slim fingers. Throughout the group the trend is toward living more and more of a truly littoral life on protected flats or beaches of muddy sand. *U. latimanus* may also be found on the banks of fresh water streams, subject to seasonal drying. Coloration, display and stridulation apparently reach their highest development in this group.

Group 6. *panamensis*. This species is so isolated from the others on the west coast that it must be placed alone. It is characterized by a flattened carapace, apparently associated with its habit of living among stones, and has strong, toothless, short, minor chelae furnished with stiff brushes, which probably help in removing from the rocks the algae upon which it feeds. It has a moderate number of spoon-tipped hairs. The burrowing instinct is feebly developed. Color very variable. Display and display coloration not observed at full development.

## VI. Key to Species of *Uca* Occurring on the West Coast of America and in the Galapagos Islands.

Including the 11 new species in the present collections, the total of apparently valid species known from the west coast of America and the Galápagos is brought to 33. Of these four—*U. galapagensis*, *U. helleri*, *U. macrodactylus* and *U. panamensis*—occur in the Galápagos, the second being indigenous.

The 22 species previously known include the 19 recognized by Miss Rathbun (1917, pp. 376 ff) and three species which have since been described, namely *U. ecuadoriensis* Maccagno, 1928, *U. inaequalis* Rathbun, 1935, and *U. deichmanni* Rathbun, 1935. *U. guayaquilensis* Rathbun, 1935, appears, from a reexamination, to be without question synonymous with *U. festae* Nobili, 1902, all being immature examples. The only recorded specimens of the latter and of *ecuadoriensis*, deposited in Turin, Italy, are unavailable for examination because of the war.

Twenty-six species are included in the present collection. All have been compared with specimens in the United States National Museum in Washington or the American Museum of Natural History, New York. Of the remaining seven known from the eastern Pacific, I have seen examples in the same institutions of all except two, *ecuadoriensis* (in Italy) and *rectilatus* (destroyed in San Francisco fire).

In making the following key an attempt was made to emphasize characteristics other than those of the major chelipeds of adult males, since these members are so often missing, gain their development so late in the life of the crab, and are useless in identifying females. With the addition of so many new, intermediate species, the use of two of Miss Rathbun's main divisions, semi-cylindrical and non-semi-cylindrical, and convex and straight antero-lateral margins, respectively, has been impracticable, except as minor subdivisions. When possible, a number of characteristics are given under each portion of the key, since crabs are so frequently damaged, and since some of the most important characters are troublesome to determine (e. g., spoon-tipped hairs and form of abdominal appendage).

In immature specimens, the form of the minor chelae, general widths of front and eyebrow and, surprisingly, the development of the arm of the abdominal appendage are the most reliable characters. Where the general group of a young specimen is in question, the number of spoon-tipped hairs on the second maxilliped is often useful, since though the full number is not developed in the young, spoon-tipped hairs are apparently never lost with growth. In the end-forms of Group 5, for example, where the spoon-tipped hairs are most highly developed, even specimens measuring 2 or 3 mm. in length have at least 25 well developed, which total at once eliminates the possibility of their belonging to the end-forms of Group 2 or Group 4.

Terms such as "width of front," "eyebrow," etc., used in the following key, are defined on page 148.

1a. Front narrow and spatuliform, less than 1/10 width of carapace.
  2a. Lateral margins either granulate or unarmed.
    3a. Abdominal appendage of ♂ thick and blunt; gonopore of ♀ with tubercle beside it.
      4a. Dorsal part of lateral margin a strong granulated line in both sexes. (Lower California—Peru)..... *princeps*, p. 170.
      4b. Dorsal part of lateral margin absent in ♂, very faint, non-granulated, in ♀. (Mexico).... *monilifera* Rathbun, 1914; Rathbun, 1917, p. 380.
    3b. Abdominal appendage of ♂ slender and tapering; gonopore of ♀ without tubercle, crescentic.
      5a. Ocular stylet in ♂ absent, or no longer than cornea. ♀ with these characters: max. lgth. 10 mm.; hairs on chelae long, close-set, those on upper edge of dactyl at least as long as dactyl's breadth; triangular suborbital region nearly naked. (G. of Fonseca—Panama) *heteropleura*, p. 171.
      5b. Ocular stylet in ♂ always present, longer than peduncle. ♀ with these characters: max. lgth. 14.5 mm.; hairs on chelae relatively short and scant, those on upper edge of dactyl shorter than dactyl's breadth; triangular suborbital region covered with short, wide-spaced hairs. (G. of Fonseca—Ecuador) *stylifera*, p. 171.

2b. Lateral margins armed with large spiniform tubercles; merus joints of legs with tubercles or spines in both sexes; short ocular stylet present or absent in ♂. (G. of Fonseca to Chile)..... *insignis*, p. 173.

1b. Front wider, increasing in width from below upward.

6a. Carapace little convex; front broad, about ⅓ carapace width; antero-lateral angles strongly produced. Small chelae short, thick, toothless, with distal hairs thick-set, covering tips, more than a third length of chelae; gape slight. Major palm without oblique ridge, its infero-proximal angle thick, projecting backward; chelae long. (G. of Fonseca—Peru)..... *panamensis*, p. 204.

6b. Not as above.

7a. Gape between small chelae slight, much less than width of middle of dactyl; serrations moderate or strong; tips dilated.

8a. Suborbital region almost or completely covered with short hairs.

9a. Orbits strongly oblique. No oblique tuberculated ridge inside major palm.

10a. Antero-lateral margin almost lacking.

11a. Palm of major cheliped much swollen; a scattering of granules on its inner surface. Spoon-tipped hairs sparse, up to about 12. (Costa Rica)
*pygmaea*, sp. nov., p. 174.

11b. Major palm not much swollen; inner surface smooth; Spoon-tipped hairs around 75. (Nicaragua, Costa Rica)
*zacae*, sp. nov., p. 175.

10b. Antero-lateral margin well developed, convex. Major chelae shorter than palm. (Ecuador) *ecuadoriensis* Maccagno, 1928, p. 49.

9b. Orbits scarcely oblique. Oblique ridge inside major palm present; major chelae longer than palm.

12a. Small chelae with plentiful hairs. Suborbital region partly naked. (Galápagos, Peru)
*galapagensis*, p. 176.

12b. Small chelae almost naked. Suborbital region densely haired. Spoon-tipped hairs from several to 20.

13a. Eyebrow not as wide as eyestalk, oblong. Oblique ridge inside major palm several tubercles wide, but obsolescent in large specimens; carpal eminence low. Gonopore with 2 or 3 tubercles on surrounding ridge. (Bahamas—Brazil; Western Mexico—Costa Rica)
*mordax*, p. 176.

13b. Eyebrow wider than eyestalk, triangular. Oblique ridge inside palm a single row of tubercles; carpal eminence high. Gonopore with single tubercle. (Lower Calif.—Panama)
*brevifrons*, p. 177.

8b. Suborbital region almost naked, with at most several rows of hairs close to orbital margin.

14a. Front narrow, 1/6 to 1/9 width of carapace. Gape between small chelae lacking in distal half, their teeth strong. Spoon-tipped hairs about 30–45.

15a. Carapace with tomentum in patches. No tooth on carpus of major cheliped. Orbits strongly oblique. Front about 1/6 width of carapace. Max. lgth. 7.3 mm. (Costa Rica)
*tomentosa* sp. nov., p. 179.

15b. Carapace without tomentum, except in young. A tooth on major carpus. Orbits little oblique. Front about 1/9 carapace width. Max. lgth. 19.5 mm. (Costa Rica, Panama). *umbratila* sp. nov., p. 181.

14b. Front wider.

16a. Front contained about 3½ times in width of carapace. Carapace moderately arched. Lateral margins anteriorly well developed, convex, curving gradually backward; posteriorly strongly convergent. 30–75 spoon-tipped hairs. Oblique ridge inside major palm strong, continued to upper margin. Merus joints of legs enlarged. (Mexico—Chile; Galápagos)
*macrodactyla*, p. 178.

16b. Not with above combination of characters.

17a. Carapace often strongly arched, but never completely semi-cylindrical. Marginal line of front distinct. Segments of abdomen of male not fused.

18a. Abdominal appendage of ♂ with arm. Eyebrow almost as wide as eyestalk.

19a. No oblique ridge inside major palm. Orbits strongly oblique; antero-lateral margins practically absent. 50–60 spoon-tipped hairs. (Costa Rica)
*argillicola* sp. nov., p. 183.

19b. Oblique ridge present. Orbits little oblique; antero-lateral margins well-developed, straight, slanting outward. About 5–10 spoon-tipped hairs.

20a. Front contained about 3½ times in carapace width. Dactyl of major cheliped about twice length of palm. Arm of abdominal appendage arising about 4½ times its own length from tip. (Gulf of California)..... *coloradensis* (Rathbun, 1983); Rathbun, 1917, p. 410.

20b. Front contained about 4½ times in carapace width. Dactyl of major cheliped about three times length of palm. Arm of abdominal appendage arising about 7 times its own length from tip (Ecuador)..... *festae* Nobili, 1902; Maccagno, 1928, p. 32.

18b. Abdominal appendage of ♂ without arm; eyebrow half or less than half width of eyestalk.

21a. Antero-lateral margins not slanting outward. Pile in 8–12 small patches on carapace. A row of tubercles along carpus of first major ambulatory. Carapace not strongly convex. (Nicaragua—Ecuador)
*inaequalis*, p. 185.

21b. Antero-lateral margins slanting outward. Pile, if present, not in many small tufts. No tubercles on carpus of first major ambulatory. Carapace strongly convex.

22a. No oblique ridge inside major palm. Ambulatories long and slender. (Costa Rica)
*tenuipedis* sp. nov. p. 186.

22b. Oblique ridge present, meeting proximal ridge at base of dactyl above. Merus of ambulatories much enlarged. (Costa Rica, Panama)
*oerstedi*, p. 184.

17b. Carapace semi-cylindrical. Marginal line of front obsolescent or absent. Segments of abdomen of ♂ fused; no arm on abdominal appendage.

23a. Eyebrow less than half width of eye stalk; spoon-tipped hairs few or absent, suborbital crenulations obsolescent except externally.

24a. Orbital angle a right angle, not produced. No large isolated tooth externally on lower orbital margin in ♂. Minor cheliped palm slender. Base of major pollex little or no deeper than dactyl at base, merging with manus dorsally in the usual concave line. (Costa Rica, Panama)
*batuenta* sp. nov., p. 187.

24b. Orbital angle acute, produced. A large isolated tooth externally on lower orbital margin in ♂. Base of major pollex broad, merging with manus dorsally in straight line continuous with its prehensile edge. Minor cheliped palm deep, swollen, especially in ♀. (Costa Rica, Panama)
*saltitanta* sp. nov., p. 189.

23b. Eyebrow at least as wide as eyestalk. Spoon-tipped hairs more than 100. Suborbital crenulations strong.

25a. Ambulatories short and stout (merus of 3rd on minor side about 2/5 of its length in ♂). Tips of minor chelae not overlapping. Regions of carapace not individually tumid, sides only moderately steep. Spoon-tipped hairs projecting beyond margin about 100–140. (Nicaragua—Panama)
*beebei* sp. nov., p. 192.

25b. Ambulatories long and slender (merus of 3rd on minor side about ¼ of its length in ♂. Tips of minor chelae overlapping. Regions of carapace strongly tumid, sides very steep. Spoon-tipped hairs projecting beyond margin about 160–250. (Gulf of Fonseca—Chile)
*stenodactyla*, p. 195.

7b. Gape between small chelae wide, at least equal to width of middle of dactyl; serrations vestigial or absent; tips of chelae usually tapering, meeting imperfectly.

26a. Orbits very oblique; carapace well arched but not semi-cylindrical.

27a. Oblique ridge inside major palm continuing only to carpal cavity. (Lower California; no specimens extant)
*rectilatus* (Lockington, 1877); Rathbun, 1917, p. 405.

27b. Oblique ridge inside palm continued to upper margin. (Galápagos only)
*helleri*, p. 198.

26b. Orbits scarcely oblique. Carapace strongly arched or completely semi-cylindrical.

28a. Eyebrow narrower than eyestalk. Weak serrations on minor chelae.

29a. Merus of ambulatories enlarged. Tip of major pollex tapering. Marginal ridge of front strong. Abdominal segments of male distinct.

30a. Antero-lateral margin straight. Upper margin of major palm with carina. Arm of abdominal appendage ends at least 3 times its own length from appendage tip. Carapace lgth. to 10 mm. (California and Mexico)
*crenulata*, p. 198.

30b. Antero-lateral margin concave; Upper margin of major palm without carina. Arm of abdominal appendage ends about 1½ times its own length from appendage tip. Carapace lgth. to 7 mm. (Costa Rica)
*limicola* sp. nov., p. 198.

29b. Merus of ambulatories slender. Tip of major pollex obliquely truncate. Marginal ridge of front obsolescent. 3rd–6th abdominal segments of ♂ more or less fused. (Costa Rica, Panama)
*deichmanni*, p. 199.

28b. Eyebrow at least as broad as eyestalk. No serrations on minor chelae. 3rd–6th abdominal segments of ♂ fused.

31a. Marginal ridge on front distinct. No oblique ridge inside major palm; major chelae shorter than palm; no stridulating ridge. (Mexico—Colombia).....*latimanus*, p. 201.

31b. Marginal ridge on front obsolescent. Oblique ridge inside major palm present; chelae much longer than palm; stridulating ridge present on lower inner side of palm.

32a. Carapace moderately swollen, the branchial, buccal and pterygostomian regions not especially gibbous. Gape between minor chelae not more than 1.5 times width of minor dactyl. Arm of abdominal appendage rudimentary. Length to 6.5 mm. (Costa Rica, Panama) *terpsichores* sp. nov., p. 202.

32b. Carapace greatly swollen, the branchial, buccal and pterygostomian regions separately greatly gibbous. Gape between minor chelae at least twice width of minor dactyl. Arm of abdominal appendage well developed. Length to 8 mm. (California & northern Mexico)..... *musica* Rathbun, 1914; 1917, p. 417.

## VII. Species of *Uca* Taken by the Eastern Pacific Expeditions of the New York Zoological Society.

### *Uca princeps* (Smith, 1870).

Text-figs. 2, 3, 5.

(see also pp. 149, 153, 156, 165, 167).

*References: Gelasimus princeps* Smith, 1870, p. 120, pl. 2, fig. 10; pl. 3, figs. 3–3c.
*Uca princeps*, Rathbun, 1917, p. 382, pl. 133; pl. 160, fig. 6.

*Range:* San Bartolomé Bay, Lower California, to Peru.

*Local Distribution:* Found on open tidal mud flats and on muddy sand beaches, usually near mangrove sprouts.

*Supplementary Specific Characters:* Abdominal appendage of male thick and blunt, with a strong curving spine near tip. Gonopore of female located close to anterior margin of third sternal segment. This location, coupled with the presence of a large tubercle beside it, at once distinguishes the females of this species from those of *U. stylifera* and *U. heteropleura*. The strong granulated line marking dorsal part of lateral margin in both sexes distinguishes the species easily from the closely related *U. monilifera*.

*Measurements:* The seven specimens taken include the following extremes of length: largest male, 24.5 mm.; larger female, 19.5 mm.; ovigerous (smaller) female, 14.5 mm.; smallest male, 15 mm.

*Color:* Displaying males, carapace length about 15 mm., observed through binoculars: Carapace purplish gray with bluish posterior margin. Major cheliped, outer side: merus basally orange, distally dark plum, as is carpus; manus, lower two-thirds bright orange, upper third white; chelae white. Major cheliped, inner side: ischium salmon orange; merus and carpus white; manus apricot buff; chelae white. Minor cheliped purplish-gray. Ambulatories purplish-gray except as follows: anterior (ventral) side of merus of first three legs on major side bright salmon orange, on minor side white. Buccal and pterygostomian regions white. Eyestalks yellow.

A much larger (24.5 mm.) male from Golfito, Costa Rica, observed after capture but while still alive differed from the males displaying at La Boca, Panama (described above) chiefly as follows: the upper part of the manus of the major cheliped was purple externally, the dactyl pinkish-white and the pollex scarlet, instead of white. The brown-flecked-with-white carapace of this specimen was obviously not in display coloration, since the crab had been captured.

Females and young grayish-brown, usually flecked with white.

*Display:* No specimens larger than about 15 mm. were seen at La Boca, but they displayed vigorously and definitely courted individual females, although none was seen actually mating. Two males were observed, to seize females after strenuous displays, and try, unsuccessfully, to drag them down their burrows. The display was as follows:

All ambulatories are held on ground, but with each gesture they are stretched upward, elevating body. Major and minor chelipeds start from position folded in front of mouth, with the carpomanus joint elevated and the chelae hanging down. The manus and chelae of both chelipeds are then extended upward and outward, being spread slowly, then brought more quickly into position. During display, the crab, elevated high on the stretching ambulatories, runs a few steps in either direction. Each display lasts about three-quarters of a second, and an almost equal time elapses between displays.

Although a few individuals were seen at La Boca on the mud flat, only those on the muddy sand beach were displaying, although they were of similar sizes.

*Breeding:* As has been indicated above, males around 15 mm. long were apparently breeding at La Boca; this was in January and February; one ovigerous female was seen (not captured) at this time. On the *Zaca* Expedition an ovigerous female was taken in March at Golfito, Costa Rica. The eggs, which measure .24 mm. in diameter after having been preserved in alcohol, number about 15,000.

*Burrow:* Of displaying, moderate-sized male in stony muddy sand: slants steeply for several inches, then turns sharply and parallels ground for several more. Of male of similar size in muddy sand: slants from surface at angle of forty-five degrees, extending six to eight inches. Of large males at Golfito on gravelly mud flat: slant from surface, measuring one to two and a half feet in length, the ends lying eight inches to two feet underground.

*Material:* A total of seven specimens was taken at Ballenas Bay and Golfito, Costa Rica, and at La Boca, Balboa, Canal Zone. Others were seen and not collected at the latter locality. Cat. Nos. 38, 355, 38588, 4135.

***Uca heteropleura*** (Smith, 1870).

Text-figs. 4A, 5.

(See also pp. 149, 150, 153, 154, 156, 165, 167).

*References: Gelasimus heteropleurus* Smith, 1870, p. 118, pl. 2, fig. 7; pl. 3, figs. 2–2b.
*Uca heteropleura*, Rathbun, 1917, p. 385, pl. 161, figs. 1–4.

*Range:* Previously known only from the Gulf of Fonseca, El Salvador. The present material extends the range four degrees southward to Panama City, Panama.

*Local Distribution:* Locally abundant on tidal mud flats. Displaying males and adult females are occasionally found on muddy sand beaches, close to the edge of the mud flats.

*Supplementary Specific Characters:* The present material agrees perfectly with the type description, except that the presence of the short style on the eye, on the side of the major cheliped, proves to be of relatively rare occurrence, and of variable rarity in different colonies. At Golfito, Costa Rica, there was one styled male to 12 styleless individuals; at La Boca, Canal Zone, the ratio was only about one in 25 styleless males, but a few miles away, at Bellavista, Panama City, on exactly similar terrain, there were 26 with styles to 48 without, a ratio of about three to five. The presence or absence of styles has absolutely nothing to do with the size of the crab: the largest with a style measures 12 mm. long, the largest without, 16 mm.; the smallest with one is 2.9 mm. long, while the smallest without is also 2.9 mm. Likewise there is no question of damaged eyes involved. Finally, the individuals with and without styles indubitably belong to the same species: every other structural detail is identical, and likewise both coloration and display. Similarly there is no difference of habitat apparent. The explanation of the apparently adventitious occurrence of the style remains, as in *U. insignis* (p. 173), a mystery.

In a typical styled example the carapace length is 10.5 mm., the style 1.44 mm., the cornea 1.73 mm., and the stalk (including cornea but excluding style) 6.72 mm. In all styled examples the proportions are about the same.

Methods of distinguishing the female of *U. heteropleura* are given in the key (p. 167). The abdominal appendage of the male is distally slender and tapering, with a well developed arm, thicker than the extreme tip, arising near the latter.

*Color:* Displaying males observed through binoculars: Carapace white. Major cheliped, externally: merus, carpus and upper half of manus purple; lower half of manus and base of pollex bright orange; tip of pollex and all of dactyl white; internally: upper inner side of merus and manus orange; otherwise much as externally. Ambulatories dark gray. Adult males on emergence at low tide are muddy brown, except the merus and manus of the major cheliped, which are yellowish-brown inside and out, and the fingers, which are white. Females plain dark brown or grayish-brown.

*Display:* During display, the crab stretches up to tip-toe, lifting first and fourth ambulatories clear of ground, standing only on second and third. At the beginning, both chelipeds are folded in front of mouth with the carpo-manus joint elevated higher than the manus and chelae, which hang downwards, clearing the ground. As the crab rises to its toes, both chelipeds are extended, the manus and chelae being first stretched out sideward, then lifted by the action of merus and carpus. The chelipeds are sometimes opened all the way, sometimes only partially, depending on the degree of excitement. In maximum display, reaching up as high as possible is the ultimate object, before the chelipeds are brought down with a jerk and folded into position. Throughout display the chelae are held slightly open, parallel. Each display lasts from one-half to three-quarters of a second, with a pause between displays of about half that length of time, the speed and frequency varying with the degree of excitement. Each display takes place in one spot, but between gestures a few steps may be taken in either direction. More than one hundred displays have been observed in swift succession. The crab usually faces in one direction during the same series.

A number of ovigerous females were seen in the Canal Zone and Panama in January and February, 1941, and males were actively displaying at this time. The single ovigerous female taken carried about 3,000 eggs. In alcohol each has a diameter of .25 mm.

*Measurements:* The 116 specimens taken include the following extremes of length: largest male, 16 mm.; largest female, 10 mm.; ovigerous female, 6.5 mm.; smallest male, 2.9 mm.; smallest female, 4.3 mm.

*Burrow:* In soft mud typical holes were remarkably shallow, slanting downward two inches from the surface, then, after a sharp bend, continuing parallel to the surface for three inches more.

*Material:* A total of 116 specimens was taken at Golfito, Costa Rica, Bahia Honda and Panama City, Panama, and Balboa, Canal Zone. Innumerable other examples were seen but not collected at the two latter localities. Cat. Nos. 38,589, 38,698, 4137, 4138.

***Uca stylifera*** (Milne-Edwards, 1852).

Text-fig. 5.

(See also pp. 149, 150, 153–156, 159, 160, 165, 167).

*References: Gelasimus styliferus* Milne-Edwards, 1852, p. 145 (109), pl. 3, fig. 3.
*Uca stylifera*, Rathbun, 1917, p. 383, pl. 134, figs. 1 and 2.

*Range:* Gulf of Fonseca, El Salvador, to Guayaquil, Ecuador.

*Local Distribution:* Usual habitat seems to be tidal mud flats, although courting males were found only on muddy sand beaches.

*Supplementary Specific Characters:* Abdominal appendage of male slender, tapering and strongly

curved distally. No subterminal arm. Methods of distinguishing the female are given in the key (p. 167). Unlike *U. heteropleura* and *U. insignis*, every male seen of this species had a fully developed style.

*Measurements:* The 24 specimens taken include the following extremes of length: largest male, 17.5 mm.; largest female, 14.5 mm.; ovigerous female, 12.5 mm.; smallest male, 6.6 mm.; smallest female, 7.4 mm. Ocular style of smallest male, 3.4 mm.; stalk and cornea together, without style, 5.1 mm.

*Color:* Displaying males, observed through binoculars: Carapace, including the sides, and buccal, pterygostomian and subhepatic regions pure white, except for a narrow band of dark purple on posterior edge of carapace. Major cheliped, external side: merus and carpus bright chrome yellow; manus orange, rarely rosy, with white tubercles, usually fading into white above; pollex brighter orange, dactyl pure white; internal side: pale yellow to salmon orange, except for lower half of manus and all pollex, which are pure orange. Merus and carpus of minor cheliped pale yellow; manus and base of chelae lemon yellow; tips of chelae orange. Ambulatories, except for anterior (ventral) side of certain meri, bright purple or lilac; anterior side of merus of first three on major side bright orange, the color fading into purple posteriorly; anterior side of merus of first two on minor side white, fading into purple posteriorly; rest of anterior faces of meri like posterior. Stalks and eyes greenish-yellow; styles clear lemon yellow. Sternum and abdomen apparently purple, the abdomen being marked with orange.

Adult males, not displaying, but apparently approaching the courting season, when exposed to full sunlight, have the carapace and underparts bright lemon yellow instead of white, and the colors of the major cheliped are paler than in displaying individuals. Males just emerged from their holes with the ebbing tide, captured males, and those far from the breeding season have carapace and eye-stalks pearl gray, while the other parts are dull brownish, grayish, purplish and yellowish, varying with the individual and circumstances.

Adult females in breeding condition: Carapace purplish-gray to grayish-white; ambulatories deep purple; manus and dactyls of chelipeds white; buccal, pterygostomian and subhepatic regions pale gray.

*Display:* Body usually not elevated at all during display, and all legs kept on ground, although body is always held fairly high. Sometimes, however, during display the crab stretches the anterior two pairs of legs, so that the anterior part of the carapace is tilted up with them, while the posterior part is lowered on the bending posterior two pairs of legs. At the beginning of display, the merus and carpus of the major cheliped are usually held almost straight out at the side, the manus and chelae being bent forward from them at right angles, the whole cheliped being held well clear of the ground. The chelae are held parallel to each other, slightly open. From this position the crab raises the manus and chelae slowly and slightly, then lowers them to the original position equally slowly, without a pause, at the rate of one complete display to about three-quarters of a second. The display is repeated at once in continuous rhythm; when undisturbed the crab makes between thirty and fifty displays, usually about forty, at a time, hopping several steps in either direction, or to the front or back, with every gesture. Then it squats down and rests for about five seconds. The see-saw motion, brought about by stretching the front legs and lowering the back ones during display, mentioned above, may be inserted without apparent extra stimulus in the midst of a series of displays, or the entire series may be of the see-saw variety. When the crab becomes especially excited during a display, having aroused the attention of a female, it raises the second or third ambulatory simultaneously on each side, not necessarily as a pair, as it extends its cheliped; they are held motionless for an instant, then lowered, and the other two members of the same two pairs repeat the performance. The effect is that of a definite, rhythmic dance step. During display the style remains erect and motionless.

*Breeding:* It seems very likely that adult males and females of this species which are ready to breed come up from the mud flats on to the relative cleanliness and firmness of a muddy sand beach to court and mate. Young ones and dull colored, non-displaying males have been found only in the mud; on the muddy sand beach at La Boca, where courtship was observed, only brightly-colored males and full grown, yet non-ovigerous, females were found. On February 9, 1941, the first *U. stylifera* was observed at La Boca on the muddy sand beach, although the beach had been under observation for two weeks previously. He was in the bright yellow phase, and did not display. The next day there were five males and five females, all well separated, the males being at least six feet apart, and all in the yellow phase; the holes of the females were each at least three feet from those of the nearest males. The following day twice as many of each sex were counted in the same area, and one of the males now had the carapace pure white instead of yellow. In the days following, roughly 12 pairs were kept under observation. It appeared that during the first two to three days after their arrival on the beach the males would swing through the yellow into the pure white phase. When the latter was reached they began displaying.

In the first week of display I could not see that any of the females paid the least attention, although the burrows of individual males and females showed an increasing tendency to be dug close to each other. Later on, during the second week, many serious courtships took place daily, although I saw actual pairing, on the surface, only once (see below). Often the female would allow the male to approach her, displaying all

the way, and stroke her at the edge of her hole (p. 156), only to disappear down it at the last moment; often, if a male tried frequently to drag a female from her hole after such withdrawal, she would wait until he had temporarily given up, and then plug up her hole for the rest of the day, even though the tide was still far out. More often still, a courtship which had reached a crucial stage would be interrupted by the approach of grackles or other birds. The male always appeared to use the greatest patience and gentleness, as though afraid that sudden motions or a show of force would ruin his chances.

One male courted two females, with holes only a foot away from him and each other, indiscriminately for a week, apparently without success. When one of the females finally moved to the far side of the colony, the male continued to court the remaining one, regularly, for an hour or two a day. At the end of another week, when observations ceased, he was still adhering to the same routine; every day the procedure would reach the stroking stage several times, but I never saw them mate, or saw her approach his hole. It is interesting that his major claw was in the process of regeneration, being only about half normal size, and was pure white, like the carapace, instead of orange and yellow. His use of it in display, however, was in nowise different from that of uninjured crabs.

The single mating I observed on the surface occurred after a large, exceptionally brilliant male had courted a female, with numerous interruptions and false starts for at least three hours. The crabs assumed the position described on page 156, holding it for three minutes.

Only once did I see a male of this species induce a female to approach his hole and actually enter it. It happened after at least four days of constantly interrupted and apparently futile courtship, and after a prolonged display on the morning when she finally approached his hole. (It is possible, of course, that she had entered also on previous days, but since I had that part of the beach under almost continuous observation during the daylight low tide at that period, it is certain that she did not remain long.) As soon as she entered his hole, the male followed. A few seconds later he emerged with a load of sand, which he dumped several inches away. He continued to enlarge the hole with 33 additional loads over a period of 20 minutes. As he descended the last time he flipped in a plug after him, and, although the tide was dead low at the time, neither crab emerged the rest of the afternoon. The next day the male was feeding, and not displaying at all. He was in very poor color, the carapace being yellowish-gray where it had been dazzling white at correspondingly low tide for a week previously. The female was nowhere to be seen, and her hole, which had been about eighteen inches from that of the male for at least five days, was eradicated by the tide. The other five females in the vicinity, known to me individually, as were the above pair, by small natural recognition marks such as damaged chelae, nicks in the carapace, etc., were all present. I dug up the hole of the male, but she was not there either. Either she had moved to an entirely different part of the beach, or—and this explanation seems likely—she had gone down to the greater moisture of the mud flat to lay and carry her eggs.

None of the females on the beach at La Boca was ovigerous. The single one in the collection was taken on a mud flat at Golfito, Costa Rica, in March. The eggs, which measured .21 mm. in diameter after having been preserved in alcohol, number about 20,000.

*Burrow:* The holes of large specimens usually extend about 6 to 12 inches straight down, then turn at right angles and continue for several inches more. Less frequently, they slope downward from the mouth at an angle of more than forty-five degrees, and then turn sharply, ending in the usual way a few inches beyond the bend.

At La Boca, displaying males sometimes occupied the same burrows for at least three weeks at a time; observation stopped at the end of this period. Females on the other hand tended to shift their position and dig new burrows much more frequently. The general trend seemed to be for a female to move her burrow closer to, or farther from, a male who had been courting her, although these observations are as yet incomplete. On the other hand, males too would sometimes move yards away, without any apparent reason, while individual females maintained the same holes for days at a time. The center of the opening of a burrow, although destroyed completely twice daily by the tide, rarely varied so much as a quarter of an inch in position from day to day.

*Material:* A total of 24 specimens was taken at Corinto, Nicaragua, at Golfito, Costa Rica, and at La Boca, Balboa, Canal Zone. Cat. Nos. 3813, 38,589, 4136.

***Uca insignis*** (Milne-Edwards, 1852).

Text-fig. 5.

(See also pp. 149, 165, 168).

*References: Acanthoplax insignis* Milne-Edwards, 1852, p. 151, pl. 4, fig. 23.

*Uca insignis*, Rathbun, 1917, p. 385, pl. 161, figs. 5–15.

*Range:* Gulf of Fonseca, El Salvador, to Chile.

*Local Distribution:* Found on open tidal mud flats and at edge of mangroves, among their shoots.

*Supplementary Specific Characters:* Two of the males in the present collection have short styles on the eye, on the side of the major cheliped, exactly similar to those sometimes found on *U. heteropleura.* The style on the largest male (length 14 mm.) is 2.21 mm. long, and the cornea 1.92 mm. The tip of the abdominal appendage is slender.

*Measurements:* The four specimens taken consist of three males, 9 to 14 mm. long, and one very immature female, 8 mm. long.

*Material:* All are from La Boca, Balboa, Canal Zone, and from Bellavista, Panama City, Panama. Cat. Nos. 4139, 4140.

***Uca pygmaea*** sp. nov.

Text-figs. 4B, 5; Pl. I, Fig. 1; Pl. II, Fig. 4.
(See also pp. 149, 161, 166, 168).

*Diagnosis:* Length under 6 mm. Carapace moderately convex; front behind eyes about 30% maximum width of carapace; orbits extremely oblique; antero-lateral margins slanting obliquely inwards immediately behind orbital angles, which are produced forward and outward into pronounced acute angles. Minor chelae serrated in middle half; gape moderate throughout to articulating tips; hairs scanty except for inner distal tuft. Major palm without oblique tuberculated ridge, which is represented only by a general scattering of granules; manus greatly swollen, but without a backwardly directed, infero-proximal projection on its outer side; dactyl about as long as palm. Merus of second maxillipeds with only about a dozen spoon-tipped hairs. Suborbital region densely hairy.

*Description:* A very small species. H-form depression shallow, regions not strongly delineated. Carapace smooth and naked except for a very sparse scattering of fine, short hairs. Hairs on legs few; several on each joint are long, bristle-like and dark brown at the roots.

Carapace moderately convex, widest at antero-lateral angles. Upper margin of orbit extremely oblique, sinuous. Anterior part of lateral margin so short as to be almost non-existent, slanting strongly inward from the angle, then turning almost at once at an extreme obtuse angle, as the usual elevated line. This marginal line stops opposite the anterior part of the cardiac region. Sides of carapace concave, moderately convergent posteriorly. Front between posterior margins of eyestalks about 30% width of carapace. Lower margin of front entirely, that of orbit almost, invisible in dorsal view. Eyebrow broad, showing considerable variation in the degree of inclination, even on opposite sides of the same crab. The lower orbital margin has crenulations strongly developed externally, but usually completely absent internally. Suborbital region densely hairy. Third to sixth abdominal segments of male partially fused.

Spoon-tipped hairs on merus of second maxilliped very few, about a dozen or less. Woolly hairs moderate in number, but not forming a conspicuous tuft on tip of palp. Ischium of third maxilliped with shallow central groove well developed, oblique, almost confluent basally with inner groove.

Minor chelae about as long as palm, with fairly strong serrations in middle half; distal fourth corneous, dilated, the tips articulating perfectly; gape moderate, extending to articulation. Hairs sparse, in an irregular oblique row across inner surface of each finger, well developed only distally where about half a dozen on the inner tip of each chela are long and bristle-like.

Large cheliped of male with arm and wrist weakly rugose, the wrist also tuberculous distally; distal upper edge of arm with two or three tubercles. Hand as deep as long, considerably swollen both externally and internally. A single row of close-set tubercles along lower margin. Dorsal crest present only as a rudimentary, non-tuberculous ridge. Coarse tubercles on the outer, upper surface, continuing over on the rounded top as slightly smaller ones, and over onto the upper half of the inner surface as enlarged tubercles again. Middle outer and inner halves of manus finely granulous, lower parts practically smooth. Inner side of manus with oblique tuberculous ridge absent. A row of minute, close-set tubercles outlining dorsal margin of carpal cavity. A row of well developed tubercles extends along proximal half of upper margin of pollex and turns at a wide angle obliquely upward and backward along distal part of manus, merging with the coarse tubercles of that area. The tuberculated ridge usually present on distal edge of palm across base of dactyl is represented only by two or three small tubercles. Dactyl about as long as palm, tuberculated dorsally in proximal region, curving downward beyond end of pollex. Pollex deeper basally than dactyl, triangular, the tip obliquely truncate. Gape moderately wide, prehensile teeth rudimentary except for several enlarged teeth on each edge, typically arranged as follows: two, well separated, near base of dactyl; one on distal third of dactyl; one near base of pollex; two on truncate tip of pollex. Triangular depression on outer base of pollex very pronounced.

Merus of ambulatories scarcely enlarged.

Abdominal appendage blunt with thick, short arm paralleling it, not protruding laterally, almost reaching its tip.

*Measurements:* Male holotype: length 5.66 mm., breadth 8.35 mm., base of manus to tip of pollex 10.84 mm. Twelve paratypes (all males): length 4.03 to 5.47 mm. In spite of their small size, the larger ones show every indication of being adult.

*Color:* Captured males in life: Carapace bronzy brown, speckled or marbled with white. Large cheliped apricot buff to chestnut, except white-tipped chelae and grayish inner surfaces. Underparts entirely grayish. Upper surface of ambulatories grayish-brown, marbled with white.

*Affinities:* This species appears to be most closely related to *U. zacae* (p. 175). It differs in the extreme obliqueness of the orbit, in the deeper, swollen palm with coarse granulation on its inner surface, and in the paucity of spoon-shaped hairs on the merus of the second maxilliped. More distantly it is related to *U. galapagensis*, *U. mordax* and *U. brevifrons*, sharing with them as with *U. zacae* the same general type of third maxilliped, minor cheliped, male abdominal appendage, broad front and hairy suborbital region, but differing most obviously in the obliqueness of the orbits and the lack of an oblique tuberculated ridge on the inner surface of the major palm.

*Local Distribution:* All 13 specimens were taken from the muddy banks of a fresh water stream. The burrows were two to three inches deep.

*Material:* All were taken at Golfito, Costa Rica.

Cat. Nos. 381,110 (holotype) and 381,111 (paratypes).

The name *pygmaea* is proposed for this species because of its small size.

### *Uca zacae* sp. nov.

Text-figs, 4C, 5; Pl. I, Fig. 2; Pl. II, Fig. 5.
(See also pp. 149, 159, 166, 168).

*Diagnosis:* Carapace moderately convex; front behind eyes slightly more than one-fourth maximum width of carapace; orbits strongly but not extremely oblique; antero-lateral margins short, straight, angled; orbital angles produced scarcely or not at all; minor chelae serrated in middle third; distal third corneous; gape moderate to articulating tips; hairs on inner surface plentiful. Oblique tuberculated ridge inside palm of major cheliped completely absent, or, rarely, represented by several rudimentary tubercles; no backwardly directed, infero-proximal projection on outer side of manus; fingers about as long as palm. Merus of second maxillipeds with many (around 75) spoon-tipped hairs. Suborbital region hairy.

*Description:* A small species. H-form depression moderately deep; regions otherwise scarcely delineated; surface of carapace smooth, naked except for a pair of tomentous patches in the H-form depression, between the branchial and anterior cardiac regions. There are also a few short hairs scattered irregularly over the carapace; hairs on legs yellowish or brownish, and mostly soft, not stiff and black.

Carapace moderately convex, widest at antero-lateral angles. Upper margin of orbit strongly oblique, especially in young, but not extremely so. Anterior part of lateral margins very short, usually straight, but sometimes somewhat rounded, sloping inward; the margin then turns at a very blunt, obtuse angle and is continued in a concave line to a point opposite the posterior portion of the cardiac region. Sides of carapace concave, moderately convergent posteriorly. Front between posterior margins of eyestalks slightly more than one-fourth width of carapace. Lower margin of front and lower edge of orbit visible in dorsal view. Eyebrow moderately broad and inclined. Lower margin of orbit with crenulations moderately developed externally, almost or completely lacking internally. Suborbital region hairy. Third to sixth abdominal segments in male partially fused.

Spoon-tipped hairs on merus of second maxilliped numerous, 55 to 85 or even more, arranged in about 9 to 11 rows, on distal three-fifths of inner edge. Woolly hairs moderate in number, not forming a conspicuous tuft on tip of palp. Ischium of third maxilliped with shallow central groove well developed, oblique, almost confluent with inner groove basally.

Minor chelae with fairly strong serrations in middle third; distal third corneous, little dilated, the tips articulating fairly well; gape moderate, extending to articulation. Hairs plentiful in an irregular oblique row across inner surface of each finger, longest and strongest distally; a similar row of shorter, fewer hairs externally.

Large cheliped of male with arm rugose, and wrist weakly tuberculate. Hand at least once and a half times as long as broad with rows of tubercles—double above and single below—forming carinas on upper and lower margins; coarse tubercles distributed over upper, outer surface; rest of the latter smooth. Inner surface without oblique, tuberculous ridge, its usual position marked only by a perfectly smooth, elevated region, except in a few rare cases where several rudimentary tubercles are present. The upper margin of the carpal cavity is marked by a single row of closely set, small tubercles. A row of well developed tubercles extends from the proximal part of the upper margin of the pollex up along the distal part of the manus until, near the dorsal margin, it splays out in a small cluster of tubercles. A short row of several very low tubercles, distal to this, parallels the base of the dactyl. Except for the tubercles and ridges described, the inner side of the manus is perfectly smooth. Dactyl as long as, or slightly longer than, palm, tuberculated dorsally in proximal region, curving downward beyond tip of pollex. Latter more slender than dactyl, obliquely truncate. Gape moderately wide; a number of coarse teeth on each finger; three basal teeth of dactyl usually somewhat larger than adjacent ones; another tooth, two-thirds of way to tip, considerably enlarged; a similar one sometimes present on pollex, halfway to tip.

Merus of ambulatories scarcely enlarged, more so in females than in males; that of third leg extends about a fifth, more or less, of its length beyond antero-lateral angle when laid forward.

Abdominal appendage of male moderately blunt distally with a well developed arm extending outwards from it at an oblique angle, terminating one and one-half times its own length from the tip.

*Measurements:* Male holotype, length 6.9 mm., breadth 11.04 mm.; base of manus to tip of pollex, 15.1 mm.; largest female (paratype), length 6.05 mm., breadth 9.12 mm.; smallest male (paratype), length, 3.3 mm., breadth 4.8 mm.; smallest female (paratype), length 3 mm., breadth 4.2 mm.

*Affinities:* This species appears to be most closely allied to *U. pygmaea* (p. 174); its resemblance to the young of *U. macrodactyla* is noteworthy (see p. 178).

*Range:* Corinto, Nicaragua, to Golfito, Costa Rica.

*Local Distribution:* The 34 specimens in the collection were taken in mangrove mud (Corinto) and on the muddy banks of fresh water streams (San Juan del Sur and Golfito). Twenty-eight of the specimens were taken at Golfito from a large colony.

*Material:* The specimens were collected at the following localities: Corinto and San Juan del Sur, Nicaragua; Golfito, Costa Rica. Cat. Nos. 381,112 (holotype male, Golfito); 381,113 (27

paratypes, males and females, Golfito); 381,114 (2 males, 2 females, Corinto); 381,115 (2 males, San Juan del Sur).

This species is named in honor of Templeton Crocker's yacht *Zaca*.

***Uca galapagensis*** Rathbun, 1902.

Text-figs. 4D, 5.

(See also pp. 149, 166, 167, 168).

*References: Uca galapagensis* Rathbun, 1902, p. 275, pl. 12, figs. 1, 2; 1917, p. 403, text-fig. 167, pl. 142. Boone, 1927, p. 273 (*part.*), not fig. 97.

*Range:* Galápagos Islands and Peru.

*Local Distribution:* Salt flats and around salt ponds.

*Supplementary Specific Characters:* Merus of second maxillipeds with 25 or less hairs having well developed spooned tips, but many more on which minute, rudimentary spoons can be distinguished. Woolly hairs present in moderate numbers. Ischium of third maxilliped with shallow, central groove traceable in distal two-fifths.

Minor chelae slightly longer than palm, with weak serrations in middle third or third quarter; distal third or quarter corneous, dilated, the tips articulating perfectly; gape moderate, extending to articulation. Hairs sparse, chiefly in an irregular, oblique row on inner surface of each finger, longest distally; externally surface of fingers naked except for a few short rows of stumps of bristles near tip.

Suborbital region sparsely to moderately hairy.

Abdominal appendages of male moderately slender, abruptly pointed at tip; arm short, thick, parallel to appendage, not protruding laterally, terminating less than its own length from tip of arm.

*Material and Discussion:* The four specimens in the collection of the Department of Tropical Research were all taken by the Harrison William Galápagos Expedition (1923) and have already been recorded by Boone (1927, p. 273). They consist of the following catalogue numbers:

No. 2139. 2 males, lengths 4.4 and 4.9 mm. South Seymour Island.

No. 2624. 2 males, lengths 9 and 11 mm. James Island.

The other specimens referred by Miss Boone to this species prove upon reexamination to be distributed as follows:

No. 2042. 1 male, length 11 mm. Eden Island: Should be referred to *Uca macrodactyla* (see p. 178). This is the specimen figured in the upper half of fig. 97, p. 272 (Boone, 1927). The other small specimen catalogued under this number has completely disintegrated, and hence has been discarded.

No Number. 1 female, length 11.5 mm. Cocos Island. *Arcturus* Oceanographic Expedition. Should be referred to *Uca panamensis* (see p. 205). This is the specimen reproduced in the lower half of fig. 97, p. 272 (Boone, 1927). Glassell (1934, p. 453) has already suggested that *U. panamensis* might be involved in this figure.

In her discussion of *U. galapagensis*, Miss Boone states (1927, p. 274) that *U. galapagensis* digs chiefly at night or in "the cool of early dawn when the tide is out . . . The huge chela of the male, and in the case of the females, either chela, form the shovel with which the sand is rolled into a pellet which is clasped by the three hinder anterior ambulatory legs, while the crab climbs out of its burrow by using its front anterior ambulatory leg and chela and its four posterior ambulatories. . ." I have never seen *U. galapagensis* alive, but all of the twenty-odd other species of *Uca* which I have observed actually digging agreed with the observations of other students of the genus in being diurnal, in never using either cheliped as a shovel, and in almost always entering the hole with the minor side going first.

Miss Boone goes on to say that "One of the uses of the 'voice,' that is, the noise caused by the stridulating ridge of the giant chela, is to warn other members of the species that their particular burrow is inhabited, a warning that is usually respected." This sentence would be true of *Ocypode gaudichaudii* and others of that genus, and probably of *U. musica* and some of its allies (see p. 165) as well, since these fiddlers have developed true stridulating ridges, in addition to the usual oblique, tuberculous ridges, with opposable rows of tubercles on the first ambulatory legs. However, in *U. galapagensis*, as in most other fiddlers, there is only the usual oblique tuberculous ridge on the large cheliped, which is in no position to be used for stridulation, but merely, along with the other ridges, bounds the area folded upon the merus.

Whatever the sources of Miss Boone's statements, they were not the field notes of Dr. William Beebe, director of the Harrison Williams and *Arcturus* Expeditions, nor those of any of his staff.

***Uca mordax*** (Smith, 1870).

Text-figs. 2, 3, 4E, 5.

(See also pp. 149, 152, 157, 166, 168).

*References: Gelasimus mordax* Smith, 1870, p. 135, pl. 2, fig. 3; pl. 4, figs. 4 and 4a.

*Uca mordax* Rathbun, 1917, p. 391, text-fig. 166, pl. 134, figs. 3 and 4.

*Range:* Previously known from the Bahamas and Gulf of Mexico to Rio de Janeiro, and from the west coast of Mexico; questionably reported from Liberia. The present expeditions have extended the eastern Pacific range about 10 degrees of latitude, from Mexico to the Gulf of Dulce, Costa Rica.

*Local Distribution:* Found among mangrove roots and in the stony mud banks of both brackish and fresh water streams.

*Supplementary Specific Characters:* Spoon-tipped hairs on merus of second maxilliped almost or completely lacking; woolly hairs moderate in number. Ischium of third maxilliped with

central groove very broad, shallow, parallel to inner groove, with which it tends to merge basally, although it is scarcely traceable so far.

Minor chelae about as long as palm with fairly strong serrations in middle third; distal third horny, dilated, the tips articulating perfectly; gape slight, extending to articulation. Hairs sparse, absent on largest specimens except for a few stumps which are usually confined to the inner tip of each chela; in the young the distal hairs, as well as a few others along the usual inner oblique rows, are well developed, and there are in addition a few forming an external row.

Suborbital region hairy.

Abdominal appendage of male thick and blunt with a thick, short arm paralleling it, not protruding laterally, almost reaching its tip. Gonopore of female marked by two or three small tubercles arising from its elevated margin.

*Measurements:* The four specimens taken are all males and include the following extremes of length: largest, 14.5 mm., smallest 8.5 mm.

*Color:* Captured, living males from muddy banks of fresh and slightly brackish streams, Negritos Island and Golfito, Costa Rica: Carapace brownish-black with fine white spots, or marbled chocolate brown and white; major chelipeds orange brown with distal part of manus orange, or entirely coral red; chelae yellowish-brown, or coral tipped with white. Ambulatories and minor cheliped dark brown, spotted with white, or buff except for coral red at base of merus. Underparts grayish-white.

*Discussion:* Examination shows that four of the eight specimens referred by Boone (1929, p. 581, fig. 17) to *U. mordax* are examples of *U. macrodactyla*, including the specimen illustrated in fig. 17a. The remaining four were never deposited at the American Museum of Natural History, and their location is unknown. This group includes the two shown in fig. 17 b and c. It is almost certain, however, that the latter two should be referred to *U. panamensis*, as suggested by Glassell (1934, p. 454).

*Material:* A total of four specimens was taken from San Juan del Sur, Nicaragua, and from Negritos Island and Golfito, Costa Rica. Cat. Nos. 381,116, 381,117, 381,118.

### ***Uca brevifrons*** (Stimpson, 1860).

Text-figs. 4F, 5; Pl. VII, Fig. 35.

(See also pp. 149, 151, 166, 168).

*References: Gelasimus brevifrons* Stimpson, 1860, p. 292.

*Uca brevifrons*, Rathbun, 1917, p. 393, pl. 138.

*Uca brevifrons* var. *delicata* Maccagno, 1928, p. 51, text-fig. 33.

*Gelasimus vocator*, Nobili, 1897, p. 6.

*Range:* Lower California to Panama.

*Local Distribution:* Found in the muddy and clayey banks of fresh water and brackish streams, close to the water level. It was collected at Port Parker at least three miles from the sea coast, in hilly country, far above tidal influence. At Golfito, on a morning after heavy rains, a large female was found on a tree trunk, five feet above the ground, in open jungle, many yards from the nearest stream.

*Supplementary Specific Characters:* Spoon-tipped hairs on merus of second maxilliped very few, not more than about 20, usually far fewer, sometimes absent, apparently from being worn off; all are located on the upper inner half of the merus; the spoons are never large and broad. Woolly hairs abundant, often thickly fringing all margins of entire second maxilliped. Apparently of the same general type are hairs from which grow one or more clusters of tiny grape-like whitish globules. The number and distribution of both these and the usual woolly variety are exceeding variable in individuals; neither sex, size, nor the degree of elongation and slenderness of the cheliped (see below) accounts for it. Ischium of third maxilliped with shallow median groove well developed, confluent basally with inner groove.

Minor chelae slightly longer than manus, with six to nine strong serrations or low teeth beginning almost at their bases and extending throughout their length as far as distal fourth, which is corneous, dilated, the tips articulating perfectly. Gape slight, extending to articulation. Hairs almost absent in large specimens, only several remaining of the usual oblique row along inner surface of each finger, and the terminal bristles being represented only by stumps. External hairs practically absent. In the young, as in those of *U. mordax*, hairs are more plentiful and longer.

Suborbital region densely hairy.

Abdominal appendage of male thick, blunt, with thick, blunt arm paralleling it, not protruding laterally, and terminating almost at its tip. Gonopore of female opening near anterior margin of third sternal segment, marked by a single low tubercle.

*Measurements:* The 48 specimens taken include the following extremes of length: largest male, 17 mm.; largest female, 18.5 mm.; ovigerous female, 15 mm.; smallest male 3.1 mm.; smallest female, 3.5 mm.

*Color:* Living, captured specimens: Three large specimens taken in as many localities but in similar habitats showed great variation. The carapace of one male was dark brown, of the next cinnamon brown with fine, inconspicuous black marblings; and of the third, the tree-climbing female mentioned above, brilliant coral red. In the first the major cheliped was coral pink with tips of chelae white; in the second it was brown, like the carapace, with only the movable finger brightly colored—apricot orange; in the third, the female, both chelipeds were coral red, like the carapace, except for the lower half of the major palm and all the chelae, which were white. Upper part of ambulatories of all three like their respective carapaces; underparts of body and ambulatories like carapace or paling to white.

*Breeding:* The single ovigerous female was taken in January, at Port Parker. The eggs, which measure .25 mm. in diameter after having been preserved in alcohol, number about 6,000. Small specimens, measuring between 3 and 6 mm., were common on Negritos Island in March.

*Young:* The smallest specimens have the carapace of practically adult appearance, except for the more oblique orbits; the major cheliped, however, shows immaturity in the complete lack of a ridge on the inner side of the manus, although the triangular elevation is beginning to be apparent even in specimens of about 4 mm., and in the shortness of the fingers with narrow gape and numerous subequal teeth. The minor chelae are hairier than in the adult, and the suborbital region less hairy.

*Burrow:* The burrows were usually from one to two feet deep, entering the bank obliquely, or with a downward turn a few inches from the mouth; the bottoms were always under water.

*Food:* At Port Parker several crabs were observed feeding on mammalian faeces on the bank of a fresh water stream. Elsewhere, however, mud pellets of the usual type were found around their holes.

*Discussion: Uca brevifrons* var. *delicata* Maccagno, 1928, described from a specimen in the Turin Museum, was originally referred by Nobili (1897) to *Gelasimus vocatur*. Maccagno states that the major chelae are much more attenuated than in typical *U. brevifrons*, and the granulation of the palm less pronounced. In the light, however, of present material, this cannot be considered a valid variety. A single large cheliped in our collection was taken from Port Angeles, Mexico, in which the attenuation is midway between the "normal" and the *delicata* form. A specimen borrowed from the National Museum at San José, Costa Rica, originally collected at Golfito, is about identical with the Panamanian specimen illustrated by Maccagno, while one of the specimens catalogued under No. 19435 at the U. S. National Museum, from the Gulf of Dulce, Costa Rica, is equally or more attenuated than the Golfito specimen; in the same jar, under the same number and collected in the same locality, are examples of the typical and of intermediate forms. There is an almost equal amount of variation between individuals from the same locality in some of the specimens in the present collection. Neither Nobili nor Maccagno gives the length of the Panamanian specimen, but all those of the *delicata* type examined by me have been among the largest. The explanation of the differences is almost certainly either age or simple individual variation, or both.

A specimen from Uvita Bay, Costa Rica, 9 mm. long, is infested with *Sacculina*.

*Material:* A total of 48 specimens was taken from Puerto Angeles, Mexico; from San Juan del Sur, Nicaragua; and from Port Parker, Negritos Island, Uvita Bay, Golfito and Parida Island, Costa Rica. Cat. Nos. 381,119, 381,120, 381,122, 381,123, 381,124, 381,125, 381,126.

***Uca macrodactyla*** (Milne-Edwards & Lucas, 1843).

Text-figs. 4G, 5.

(See also pp. 149, 159, 166–168).

*References: Gelasimus macrodactylus* Milne-Edwards & Lucas, 1843, p. 27; 1847, pl. 11, fig. 3.
*Uca macrodactylus*, Rathbun, 1917, p. 404, pl. 143.
*Uca galapagensis*, Boone, 1927, p. 271, fig. 97 (part.).
*Uca mordax*, Boone, 1929, p. 581, fig. 17a. (See *Discussion* on p. 177 of present paper.)

*Range:* Guaymas, Mexico, to Valparaiso, Chile. Galápagos (see below).

*Local Distribution:* Found on tidal mud flats.

*Supplementary Specific Characters:* Spoon-tipped hairs on merus of second maxilliped moderately numerous, usually between about 60 and 75, with most of the spoons large, broad and well developed; all are located on distal half of merus on its inner margin; they are arranged in 8 to 10 rows. Woolly hairs variable in number and arrangement, but generally abundant; the stems of many of the spoon-tipped hairs are usually woolly also. Ischium of third maxilliped with median groove rudimentary, present only distally where it forms a marginal depression.

Minor chelae slightly longer than manus, with middle half or less strongly serrated or toothed, and distal fourth corneous. Distal third dilated, the tips articulating perfectly. Gape slight, extending to articulation. Long, soft hairs present, chiefly in an oblique row along inner margin of each chela, longest and most close-set distally. A row of similar hairs close to external margin of prehensile edge of each chela. Most of the hairs on the chelae in any row are grouped into short lines of three or four each.

Suborbital region naked, except for a few hairs immediately behind crenulated anterior margin.

Abdominal appendage of male moderately slender, tapering abruptly distally to a pointed tip. Arm short, blunt, paralleling main stem, not protruding laterally, terminating about its own length from tip.

*Size:* The 28 specimens taken include the following extremes of length: largest male, 11 mm.; largest female, 9 mm.; smallest male, 4.5 mm.; smallest female, 4 mm. No ovigerous females were seen.

*Color:* Living, captured males: plain dull brown, except for the major cheliped, which is whitish.

*Young:* The smallest specimens taken differ from the adults most noticeably in the more oblique orbits, lack of an oblique ridge on the manus of the major cheliped, and short fingers with slight gape. On the other hand, they bear a remarkable resemblance to specimens of *U. zacae*, and care is needed to distinguish the two. Young *macrodactyla* have the orbits less oblique, the fingers shorter than the palm, and the merus of the ambulatories of both sexes dilated, while the details of the grooving of the third maxilliped and the form of the abdominal appendage are helpful checks in dubious cases.

*Discussion:* The major chelae vary considerably in length even in adults. Long-fingered examples have been compared with specimens in the U. S. National Museum which were included by Miss Rathbun in material for her monograph (1917). Although her illustrations were taken from a shorter-fingered example, the museum specimens include forms identical with ours. The differences, as in the similar case of *U. brevifrons*, are doubtless explained either by simple individual variation or, more probably, by the greater age of the long-fingered specimens.

A reexamination of the specimens referred by Boone (1927, p. 271 ff., fig. 97) to *U. galapagensis* shows that one male, 11 mm. in length (No. 2042), from Eden Island, Galápagos, is an example of *U. macrodactyla* and not of *U. panamensis*, as suggested by Glassell (1934, p. 453). Although this Galápagos example of *macrodactyla* differs slightly from the typical mainland form, especially in having a slightly broader front and more projecting orbital angles, the distinctions seem too slight to be used as the basis for establishing a new form, particularly since only the single specimen has been taken.

*Material:* In addition to the Galápagos example mentioned above, a total of 28 specimens was taken from Tenacatita Bay, Mexico (1 young male, Cat. No. 381,127) and Corinto, Nicaragua (Cat. No. 381,128).

### ***Uca tomentosa*** sp. nov.

Text-figs. 4H, 5, 6.

(See also pp. 149, 166, 168).

*Diagnosis:* Carapace strongly convex, but not semi-cylindrical; front between eyes (measured between posterior margins of eyestalk bases) one sixth or less maximum width of carapace; antero-lateral margins short, straight, angled. Minor chelae strongly serrated in middle half, tips widely dilated, perfectly articulating; gape very slight or absent in distal two thirds. Major palm with oblique ridge well developed, continued to upper margin. No spine on carpus of major cheliped. Merus of ambulatory legs enlarged. Short, nap-like pile in reticulated pattern on carapace; black, stiff, isolated hairs on carapace and legs.

*Description:* A small species. H-form depression shallow, regions scarcely delineated; surface smooth, with short, thick, brownish, nap-like tomentum on branchial regions in a reticulated pattern of varying extent; sometimes it partly covers also the mesogastric, cardiac and hepatic regions. Major carpus similarly pilose, especially on upper edge and at articulation with manus. Isolated, stiff black hairs of various lengths are scattered sparsely on carapace, sternum, abdomen, eyestalks, undersides of ischia and meri of minor chelipeds and ambulatories, and on all sides of carpi and mani in both sexes; in the male several very short, black hairs occur near the articulation of the major carpus and manus.

Carapace widest at antero-lateral angles, Anterior part of lateral margins very short. straight, only about three-fifths width of front between eyes, and scarcely convergent; the margin then turns at an obtuse angle and is continued in a concave line to a point opposite middle of cardiac region. Sides of carapace concave, scarcely convergent posteriorly. Front between eyes one-sixth or less width of carapace. Lower margin of front invisible, that of orbit visible, in dorsal view. Eyebrow moderately broad, little inclined. Upper margin of orbit moderately oblique, sinuous; antero-lateral corner a right angle. Lower margin of orbit crenulated throughout. Suborbital region naked except for a single row of short hairs along crenulated margin. All abdominal segments distinct.

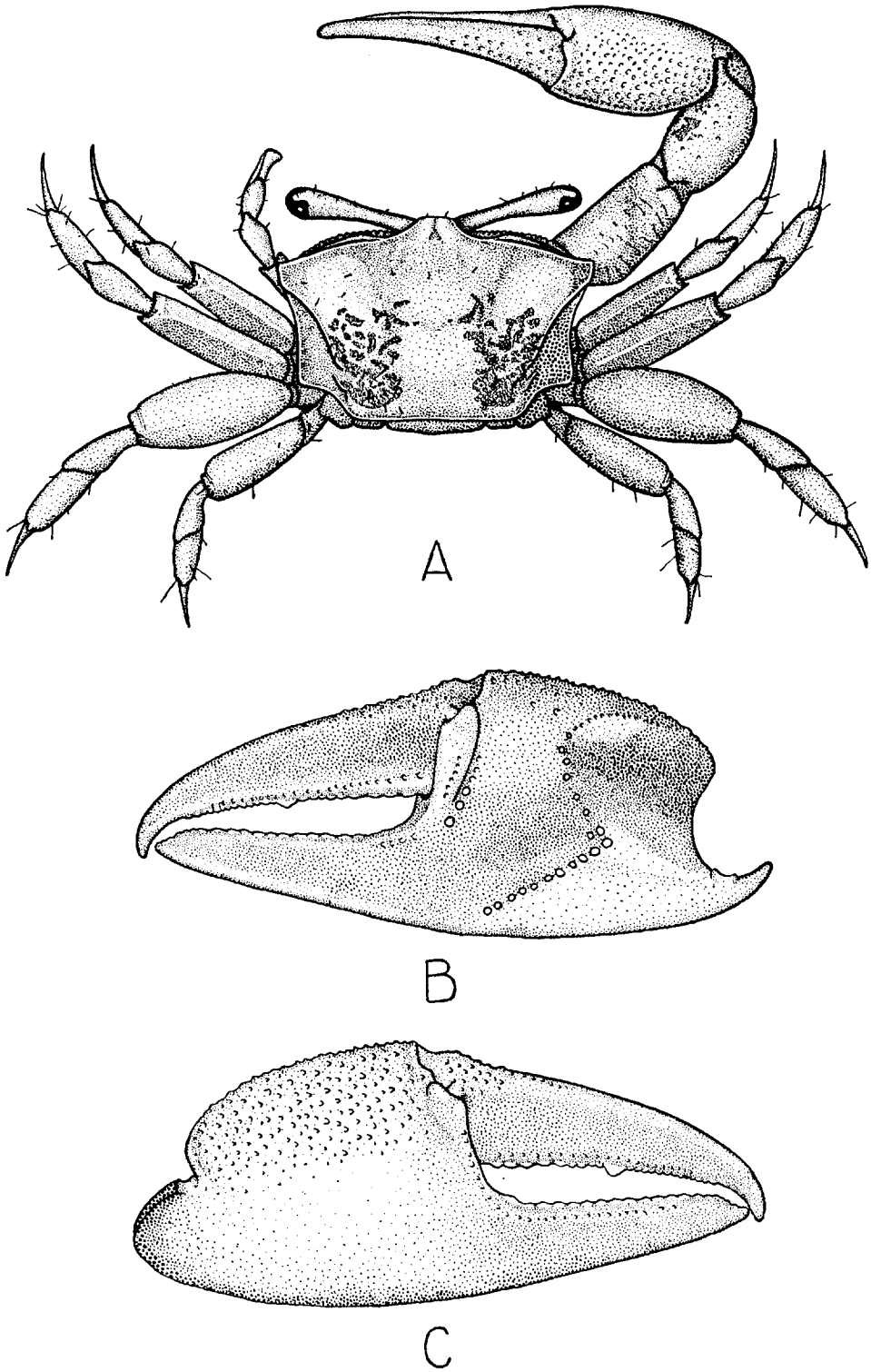
Spoon-tipped hairs of second maxilliped moderately numerous, numbering about 30 to 45, arranged in six or seven rows on anterior half of inner edge of merus. Woolly hairs plentiful, in a conspicuous group on tip of palp and along distal inner edge of merus, as well as in the more usual localities. Ischium of third maxilliped with central groove represented only by a rudimentary depression in distal margin; basally the ischium is much flattened, almost concave.

Minor chelae strongly serrated or toothed in middle half; distal fourth corneous, widely dilated, the tips articulating perfectly; gape in basal portion slight, decreasing abruptly so that distal two-thirds are almost or quite in contact; an oblique row of grouped hairs on inner surface of each chela well developed, especially distally. External surface of chelae almost or completely hairless.

Large cheliped of male with arm and wrist faintly rugose. Hand not much longer than broad, with a low carina above; upper outer surface with coarse tubercles; rest of outside smooth. Inner surface with an oblique ridge of strong tubercles extending obliquely upward from base of pollex to carpal cavity, and continued by weaker tubercles around cavity to upper margin. Carpal eminence moderately high. A weaker, broken, tuberculated ridge extending from upper, proximal side of pollex to point on manus opposite middle of dactyl base. A third row of about six still weaker tubercles, distal to the end of the latter series, parallels the articulation of manus with dactyl. Upper, inner side of manus with a few tubercles; except for these and the tuberculated ridges, the inner surface is smooth. A row of tubercles extends along outer upper edge of pollex and its base. Dactyl slightly longer than palm, gape moderately slight, fingers not very slender, with many similar, tubercular teeth; only one is enlarged, located slightly beyond middle of prehensile edge of dactyl. Proximal half of dactyl tuberculated dorsally; a longitudinal row of tubercles on its outer surface, just above prehensile edge, extending three-fourths of distance to tip; a similar ridge on inner surface.

Merus of ambulatories much enlarged; that of third leg extends very slightly beyond antero-lateral angle when laid forward.

Abdominal appendage of male with tip and arm both moderately slender, the arm terminat-




Text-figure 6.

*Uca tomentosa*, holotype. Length of carapace 6.6 mm. **A**, dorsal view; **B**, major cheliped, inner view; **C**, same, outer view.

ing a little more than its own length from tip of appendage, and extending slightly outward from it.

*Measurements:* Male (holotype): length of carapace, 6.6 mm., breadth 10.2 mm.; base of manus to tip of pollex 14.5 mm.; largest female (paratype): length of carapace 7.3 mm., breadth 11.9 mm.; ovigerous female (paratype): length of carapace 6.24 mm., breadth 9.7 mm. The two remaining specimens, both non-ovigerous females (paratypes), measure 5.6 and 6.1 mm. in carapace length, respectively.

*Affinities:* In general characteristics this species seems to be most closely related to *U. thayeri*, although its straight, angled, antero-lateral margins, little convergence posteriorly, broader fingers with narrower gape and differently formed prehensile teeth, its black hairs and smaller size all distinguish it. The similarity of carapace pile in the two species is notable. It also has affinities to *U. umbratila* (see below).

*Material:* A total of five specimens, including an apparently adult male (the holotype), one ovigerous female (paratype) and three non-ovigerous females (paratypes) were taken from clay-like mud flats among mangroves at Puntarenas, Costa Rica. Cat. Nos. 381,132 (holotype) and 381,133 (paratypes).

The name *tomentosa* is given to this species because of the distinctive pile on the carapace.

### ***Uca umbratila*** sp. nov.

Text-figs. 4I, 5, 7; Pl. VII, Fig. 34.
(See also pp. 149, 159, 166, 168).

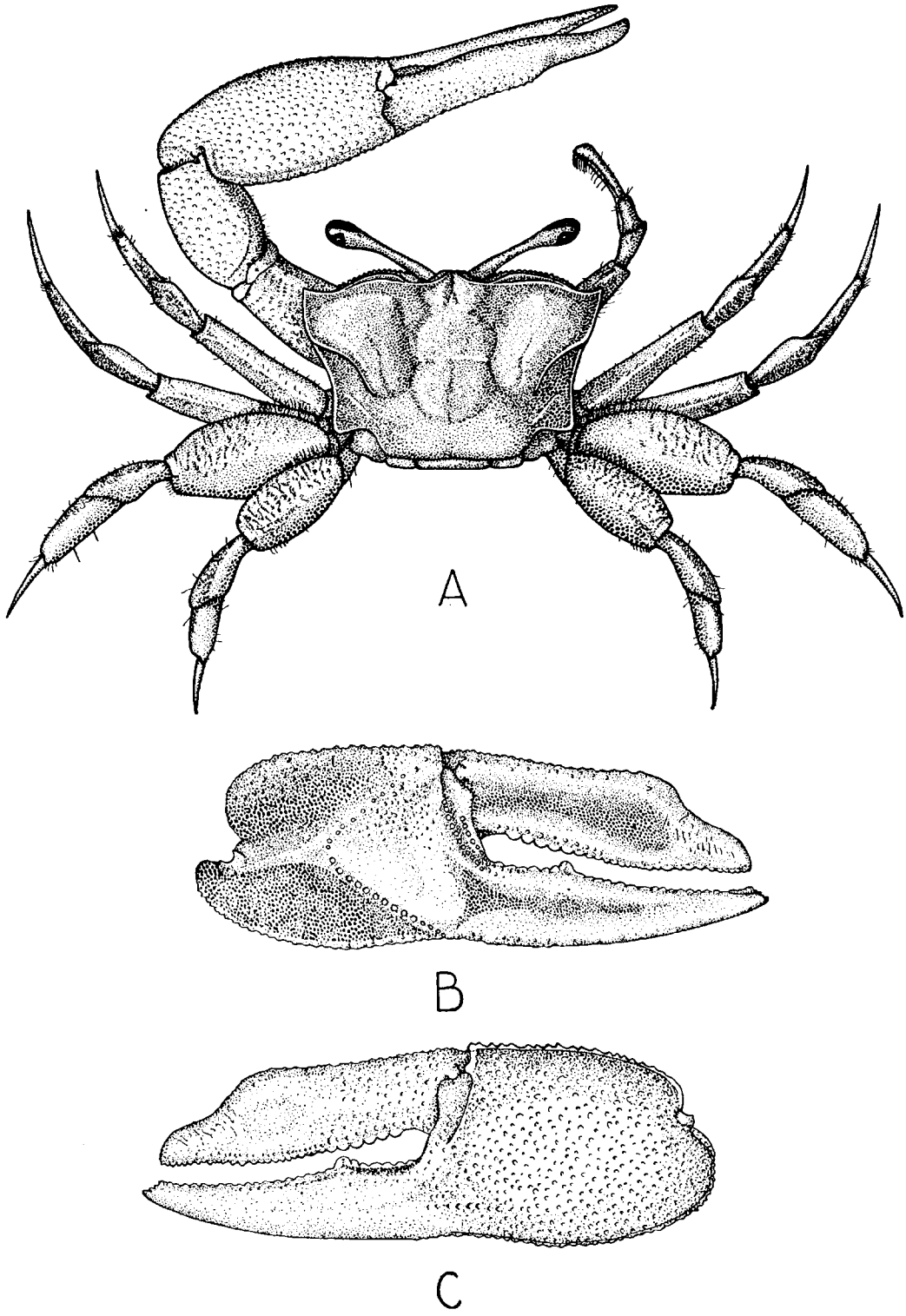
*Diagnosis:* Carapace moderately convex; front between posterior margins of eyestalk bases about one-ninth maximum width of carapace; antero-lateral margins moderately short, straight; carapace little convergent posteriorly; merus of ambulatory legs greatly enlarged. Minor chelae strongly serrated in distal two-thirds, the serrated portions in contact when chelae are closed; tips widely dilated, articulating perfectly. Oblique ridge inside major palm well developed, continuing to upper margin, but weak in upper portion; a strong carpal spine; palm massive; fingers broad, compressed, gape slight.

*Description:* A large species. H-form depression shallow, regions of carapace poorly delimited. Carapace smooth and naked. Greatest width at antero-lateral angles. Anterior part of lateral margins straight, little convergent (sometimes one side is very slightly convex), short, only about half again as long as width of front between the eyes; the margins then turn at obtuse angles and are continued in concave, rather strongly convergent lines to points opposite middle of cardiac region. Sides of carapace concave, scarcely convergent. Front between eyes contained about 9.5 times in width of carapace; a transverse, marginal ridge or line is far removed from distal edge. Lower margin of front strongly bent down, invisible in dorsal view. Eyebrows moderately broad; upper margins of orbits scarcely oblique, sinuous; antero-lateral corners acute angled, projecting forward; lower margins of orbits crenulated throughout, visible from above. Suborbital region naked except for a single row of short hairs along crenulated margin. All abdominal segments distinct.

Spoon-tipped hairs on merus of second maxilliped moderately numerous, about 30 to 40, arranged in six to eight uneven rows on distal half of inner edge; many of the spoons are very small in this species. Woolly hairs numerous, including a conspicuous tuft on tip of palp. Ischium of third maxilliped with central groove represented only by a tiny shallow depression on anterior margin; basal portion of ischium much flattened, somewhat concave.

Minor chelae slightly longer than palm, strongly serrated in median third, this portion being in contact when chelae are closed; gape basal to this slight; corneous tips widely dilated, articulating perfectly; a row of long hairs, longest distally, on inner side in short groups; a row of short hairs along outer surface, near prehensile edges; a fringe of hairs along profiles.

Large cheliped of male with arm strongly rugose, dorsally finely tuberculate. Wrist tuberculate externally; internally, at lower edge of articulating ridge, is a strong, conspicuous tooth. Hand considerably longer than broad, quadrilateral, with a carina above and below, the upper one overhanging the carpal cavity proximally. Entire outer surface of hand coarsely tuberculate, the tubercles being larger dorsally. Inner surface of palm with an oblique, strongly tuberculated ridge from base of pollex to carpal cavity; from there it continues upward at about a right angle almost to upper margin, where it breaks up into an irregular scattering of tubercles, the most proximal of which technically continue the ridge to the upper margin. A second strong tuberculated ridge extends from upper proximal side of pollex, close to distal edge of manus up to a point on manus opposite upper part of dactyl base. A third ridge of five strong tubercles, distal to end of the latter series, lies parallel between it and articulation of manus with dactyl. Space between carpal cavity and base of dactyl weakly tuberculated, in addition to tubercles of the three ridges; inner surface of manus otherwise smooth; carpal eminence moderate. A row of tubercles extends along outer upper edge of pollex and its base. Fingers broad and flattened; gape very slight. Dactyl slightly longer than palm, its abruptly constricted tip having, in the holotype, been regenerated, or damaged while still soft. In immature males the dactyl tapers and curves slightly downward distally, in the usual fashion. Prehensile tubercles similar, larger proximally than distally, except for one, much enlarged, on pollex, one-third of distance from its base. Proximal half of dactyl tuberculated proximally and externally. A longitudinal row of small tubercles on its outer surface just above prehensile edge, extending almost to tip; a similar, but shorter, row on inner surface. Proximal halves of dactyl and pollex noticeably excavated, the deepest hollow being triangular, at junction of manus and pollex.




Text-figure 7.

*Uca umbratila*, holotype. Length of carapace 17.5 mm. **A**, dorsal view; **B**, major cheliped, inner view; **C**, same, outer view.

Merus of ambulatories much enlarged, more pilose in female than in male on upper (posterior) margins; merus of third leg extends very slightly beyond antero-lateral angle, when laid forward.

Abdominal appendage of male with tip and arm both moderately slender, tapering distally, the arm terminating a little more than its own length from the tip of the appendage, and extending slightly outward from it.

*Measurements:* Male (holotype): length of carapace, 17.5 mm., breadth 29 mm., base of manus to tip of pollex 48 mm.; female (paratype): length of carapace 19.5 mm., breadth 30 mm.; smallest male, length 3.65 mm.; smallest female, length 3.17 mm.

*Color:* Immature males and females observed through binoculars: dark gray-brown all over, except distal part of major manus, and all of dactyls, outside and in, which are all yellowish-white.

*Young:* The carapace and upper surface of the ambulatories of specimens up to a length of about 10 mm. are densely covered with short pile. Even in the smallest the orbits are scarcely oblique. The front is relatively wider than in adults, and, as usual, the inner surface of the major palm is smooth and the fingers short. The carpal tooth is undeveloped in the smallest. The tips of the major chelae are semi-spooned and haired, similar to the minor chelae. These young were all taken at La Boca, in January and February, when they were very abundant; not a single adult was seen at this time.

*Affinities:* This species is most closely related to *U. thayeri* Rathbun from the Atlantic and *U. tomentosa* (p. 179) from the Pacific. The general shape of the carapace, the narrowness of the front, and the breadth and tomentosity of the ambulatories are similar in all. *U. umbratila* has the orbits less oblique than the other two, however, lacks tomentum on the carapace in the adult, has a narrower front, and has a carpal tooth. It differs further from *U. thayeri* in the more definitely angled antero-lateral margins with projecting antero-lateral angles, in the broader, flatter fingers of the major cheliped, in their smaller gape, and in the rougher merus, carpus and manus.

*Range:* From Puntarenas, Costa Rica, to Balboa, Canal Zone.

*Local Distribution:* All were found in deeply shaded mangrove mud. The male holotype and large female paratype were taken at Puntarenas in a single hole.

*Material:* The 37 specimens were distributed as follows: holotype male (Cat. No. 381,129) and one paratype female (Cat. No. 381,130) from Puntarenas, Costa Rica; one adult female, in very poor condition (Cat. No. 381,131), from Ballenas Bay, Costa Rica; 34 young, males and females (Cat. No. 4118) from La Boca, Balboa, Canal Zone.

The name *umbratila* is given to this species because all of the specimens were taken in deep shade.

***Uca argillicola*** sp. nov.

Text-figs. 4J, 5; Pl. I, Fig. 3; Pl. II, Fig. 6.
(See also pp. 149, 161, 166, 168).

*Diagnosis:* Carapace strongly convex, but not semicylindrical; front behind eyes about a fifth maximum width of carapace; orbits strongly oblique; antero-lateral margins extremely short, almost non-existent, continuing backward and inward as an elevated line almost immediately behind orbital angle, which is produced slightly forward and outward into an acute angle. Minor chelae strongly serrated except for horny tips, gape very slight, hairs scanty except for inner distal tuft. Oblique tuberculated ridge inside major palm absent, represented only by a scattering of granules; no backwardly directed, infero-proximal projection on outer side of manus, although the manus as a whole is somewhat swollen externally; palm deep, fingers shorter than palm. Merus of second maxilliped with about 50 to 60 spoon-tipped hairs. Suborbital region deeply depressed, almost naked.

*Description:* A small species. H-form depression very shallow; regions scarcely delineated; carapace smooth and naked. Hairs on legs sparse, soft and brown.

Carapace very convex, but not semi-cylindrical; widest at antero-lateral angles. Anterior part of lateral margins so short as to be almost non-existent, turning inward and backward in the form of the usual ridge practically at the antero-lateral angle; there may be slight variation in this character on two sides of the same crab. The marginal line stops opposite middle of cardiac region. Sides of carapace concave, moderately convergent posteriorly. Front between posterior margins of eyestalks about one-fifth width of carapace. Eyebrow broad, almost as broad as adjacent portion of eyestalk. The lower orbital margin has fine, low, blunt crenulations throughout its length. Suborbital region deeply depressed, naked except for one or two rows of hairs immediately behind crenulated margins. All abdominal segments distinct.

Spoon-tipped hairs on merus of second maxilliped about 50 to 60, arranged in about six or seven rows, present on slightly more than distal half of inner edge. Woolly hairs moderately few in number. Ischium of third maxilliped with central groove represented only by a marginal depression.

Minor chelae slightly longer than palm, with strong serrations or teeth throughout its length, except for a variable, very short distance proximally and the usual corneous distal fourth or fifth. Distal third dilated, the tips articulating perfectly. Gape very slight. An oblique row of sparse hairs on inner surface of each finger, thickening in length distally; a few very short hairs externally near prehensile edges.

Large cheliped of male with arm rugose, and wrist weakly rugose and tuberculated. Hand somewhat swollen externally, once and a third times as long as broad, with a low, tuberculated crest on the upper, and a row of tubercles along

the lower margin; fine tubercles, largest dorsally, are distributed over the outer surface. Inner surface without an oblique, tuberculated ridge; the latter is represented only by an irregular band of scattered granules. Upper margin of carpal cavity bounded by a single, elevated row of minute, close-set tubercles. A row of well-developed tubercles extends along the proximal half of upper margin of pollex and turns obliquely upward and back along distal part of manus, terminating in a cluster of fine tubercles a short distance from dorsal margin. Distal to this, a short row parallels base of dactyl. There is a scattering of fine granules across upper, inner surface of palm. Dactyl slightly shorter than palm, tuberculated dorsally, in proximal region, curving downward beyond tip of pollex. Both dactyl and pollex are rather deep. Tip of pollex obliquely truncate and denticulated. Gape moderate; prehensile edges with low, blunt, similar teeth, except for the enlarged, basal tooth of the dactyl, and two others opposite dorsal end of pollex.

Merus of ambulatories moderately enlarged in both sexes; that of third leg extends between a fourth and less than a fifth of its length beyond antero-lateral angle when laid forward.

Abdominal appendage of male moderately slender, tapering distally to a rounded tip; arm well developed, projecting at an angle of almost 45 degrees, terminating about one and a half times its own length from tip of appendage.

*Measurements:* Male holotype, length 7.8 mm., breadth 12.2 mm., base of manus to tip of pollex, 13 mm.; female paratype, length 7.3 mm., breadth 10.75 mm.; female paratype, length 5.57 mm., breadth 8.45 mm.

*Color:* Living specimens, observed before capture: clear, creamy white except that the entire dorsal portions of both chelipeds in both sexes are apricot buff. The color blended well with the yellowish-white clay bank in which they lived.

*Affinities:* This species appears to be a primitive form related on the one hand to *U. pygmaea* and its allies and on the other to the group containing *U. oerstedi* and related forms. Its strongly serrated minor chelae and narrow front distinguish it at once from members of the first group, while its oblique orbits and lack of a ridge on the major cheliped differentiate it from the second, as well as from the more distantly related *U. tomentosa* and *U. umbratila*.

*Local Distribution:* The three specimens in the collection were taken from yellowish-white clay banks above a slightly brackish stream. The burrows were about three inches deep. The crabs were observed to be feeding by sifting organic matter from the clay at the mouths of their burrows in typical fiddler fashion.

*Material:* All were taken at Golfito, Costa Rica. Cat. Nos. 381,134 (holotype) and 381,135 (paratypes).

This species is named *argillicola* in reference to its occurrence in white clay.

***Uca oerstedi*** Rathbun, 1904.

Text-figs. 2, 3, 4K, 5.

(See also pp. 149, 153, 154, 159, 166, 169).

*References: Uca oerstedi* Rathbun, 1904, p. 161; 1917, p. 414, pl. 152, figs. 1 and 2.

*Range:* Previously known only from the type material, taken at Puntarenas, Costa Rica; the specimens in the present collection were taken in Panama and the Canal Zone.

*Local Distribution:* Common in February on open mud flats at Old Panama, near the mouth of a stream; uncommon at La Boca, Canal Zone, on open mud flats and among unshaded mangrove shoots.

*Supplementary Specific Characters:* A variable amount of pile is present near center of carapace, usually in two large patches, in all specimens in this collection. The larger male paratype examined at U. S. National Museum, however, had no pile.

Well developed, spoon-tipped hairs on merus of second maxilliped numbering less than 20, usually less than 15. Woolly hairs present in moderate numbers. Ischium of third maxilliped with central groove represented only by a well developed, distal, marginal depression.

Minor chelae slightly longer than palm, strongly serrated or toothed at least in middle third; distal third dilated, horny, the tips articulating perfectly. Gape in basal third slight; prehensile edges of distal two-thirds almost in contact. Oblique row of hairs along inner margins well developed, longest and strongest distally, a few very short hairs externally near prehensile edges, and along profiles.

Maximum width of eyebrow less than that of adjacent section of eyestalk. Suborbital region depressed, naked except for a row of hairs immediately behind crenulated margins.

Abdominal appendage of male moderately slender, the distal fifth curved strongly forward, scarcely tapering distally. Arm absent, represented only by a few bristles arising from a shelf slanting obliquely toward base of appendage, at point where appendage bends sharply, about four-fifths of distance to tip.

*Measurements:* The 21 specimens taken include the following extremes of length: largest male 7.2 mm.; largest female (ovigerous), 6.8 mm.; smallest male, 3.1 mm.; smallest female, 3.74 mm.

*Color:* Displaying males observed through binoculars: carapace, backs of ambulatories, buccal region, and upper and outer surfaces of all of major cheliped except dactyl dull plum purple. Dactyls of both major and minor chelipeds white inside and out. All remainder of inner surface of chelipeds, pterygostomian and subhepatic regions, and anterior (ventral) surface of ambulatories turquoise blue, the anterior sides of meri being brightest of all, approaching peacock blue.

*Display:* Body held fairly high, all ambulatories remaining on ground. Large cheliped, from rest position flexed in front of mouth, opens slowly outward and slightly upward, the minor

cheliped meanwhile performing a similar motion. With no pause but a slight downward jerk, they are returned in the same plane to the crooked position. There is a short rest before the display is repeated. Including the rest, each display lasts about one and a half seconds. Several steps to one side or the other are sometimes taken, the crab usually coming slowly around the hole during a series of displays or, if he stays in the same place, the anterior ambulatories are vibrated in the midst of each display, when the chelipeds are widely spread, so that the peacock blue of the quivering meri is most conspicuous.

*Breeding:* Males were seen displaying and females showing interest throughout February in Panama. A single ovigerous female was taken, although others were seen. The eggs, after being preserved in alcohol, measure .25 mm. in diameter and number about 4,000.

*Material:* A total of 21 specimens was taken at La Boca, Balboa, Canal Zone, and at Old Panama, Panama. Cat. Nos. 4119 and 4120.

***Uca inaequalis*** Rathbun, 1935.

Text-figs. 4L, 5; Pl. II, Figs. 8, 9; Pl. III, Fig. 12.
(See also pp. 149, 153, 165, 166, 169).

*Reference: Uca inaequalis* Rathbun, 1935, p. 52.

*Range:* Previously known only from the holotype, taken at Guayaquil, Ecuador. The present collection was made between Corinto, Nicaragua, and the Canal Zone.

*Local Distribution:* Found in mud among mangroves and, more rarely, in open tidal mud flats.

*Supplementary Specific Characters:* The present material has been compared with the holotype at the U. S. National Museum and found to agree perfectly. In the light of these additional 50 specimens, Miss Rathbun's preliminary description may be amplified as follows:

There are usually 12 or more, rather than 8, pilous elevations on the carapace in the male. In the female these elevations are less well developed and usually almost naked. In both sexes, but especially in the male, single hairs are irregularly scattered, very sparsely, over the carapace. Carapace only moderately convex. Front behind eyes slightly less than one-third width of carapace; orbits little oblique; anterolateral margins straight, continuing backward with an angular turn; carapace moderately convergent posteriorly. Front entirely visible in dorsal view; eyebrow not nearly as wide as adjacent portion of eyestalk. Lower margin of orbit projecting, entire, except for several wide teeth, variable in size and number, on excavated, external portion. Suborbital region naked except for a few short hairs usually occurring just behind orbital border. Abdominal segments distinct.

Spoon-tipped hairs on merus of second maxilliped about 15 to 25. Woolly hairs moderately abundant. Ischium of third maxilliped with central groove represented only by a distal marginal depression.

Minor chelae almost once and a third times length of palm, very slender, strongly serrated or toothed in third and fourth fifths; distal fifth dilated, horny, the tips articulating perfectly. Gape slight as far as serrations, practically nonexistent thereafter. Both chelae covered sparsely with short hairs. Among these, the usual oblique row on inner face of each chela is not conspicuous except for the elongated distal hairs.

In the major cheliped, anterior half of carpus and posterior part of manus densely clothed externally with short pile, as is outer side of proximal two thirds of gape between chelae. Tuberculated ridge on inner surface of palm continuing only to carpal cavity, very oblique, running almost parallel to lower margin of manus; a rudimentary ridge on palm parallel to base of dactyl, then continuing down and out along upper inner edge of pollex as a well developed row of tubercles. Upper margin of palm distinctly bent over and flattened. Upper, outer portion of palm and upper, proximal part of dactyl with fine, rudimentary granulation. Inner, lower, proximal face of manus coarsely granulated. The granules, although not arranged in a linear series as in the stridulating ridges of *U. musica* and *U. terpsichores*, are nevertheless similarly complemented by a sometimes irregular row of seven to nine granules on carpus of first ambulatory on side of major cheliped; on distal end of merus of same ambulatory there are in addition usually three or four granules arranged in an angle or curve. The entire apparatus is similar to that found in *limicola* and *deichmanni*, but is better developed.

Major dactyl slightly longer than palm, curving distally over tip of flattened, triangular pollex; gape slight, with many similar, tubercular teeth, of which one on each finger, slightly beyond middle, is enlarged. Merus of ambulatories slightly enlarged in both sexes; in the male, that of the third extends about one-third its own length beyond antero-external corner of orbit when leg is laid forward, but in female only about one-fourth or one-fifth of its length.

Abdominal appendage of male slender, tapering distally, with arm completely lacking, represented only by a few hairs and an abrupt narrowing at beginning of distal seventh. The latter fraction is more strongly curved than the rest of the appendage, which, from the base, arches gradually forward.

*Size:* The 50 specimens taken are all smaller than the 8 mm. holotype. They include the following extremes of length: largest male, 6 mm.; largest female, 5.3 mm.; ovigerous females 4.1 to 5.3 mm.; smallest male, 2.57 mm.; smallest female, 2.9 mm.

*Color:* Displaying male observed through binoculars: carapace dark brown marbled with white. Major cheliped plain dark brown except as follows: upper surface of merus, carpus, manus and dactyl base rich chestnut; lower outer half of manus chestnut; distal half of dactyl and all of pollex white. Anterior (ventral) surface of meri of at least anterior two, and possibly all, pairs of ambulatories dark purple; ambulatories

otherwise dark brown marbled with white, like carapace. Buccal and pterygostomian regions brown. Sternum and abdomen apparently bluish-white.

*Display:* The display of only one individual was observed, on February 19, and the following observations are incomplete.

Body elevated on all four pairs of legs during each display. Large cheliped, from rest position flexed in front of mouth, opens very slowly outward and upward, making a conspicuously circular gesture. At peak it pauses infinitesimally and is then brought rapidly down, not so fast as to give the effect of a jerk. Occasionally the cheliped is brought to the ground and crooked well in front of its usual position; it is then brought back into place with a series of several thumpings of the ground, each bringing it closer to the mouth. This seems to occur when the crab is most excited. The whole display is exceedingly slow, occupying more than a second, with a pause of usually one or two seconds between displays.

*Breeding:* Four ovigerous females were taken in February and March, in Costa Rica and Panama. The eggs measure .24–.27 mm. in diameter, after having been preserved in alcohol, and number between 700 and 1,500.

*Young:* Although small examples of this species show the usual characteristics of many immature *Uca*, including a large eye, more oblique orbits, oblique antero-lateral margins scarcely distinguishable from the sides of the carapace, and small, short-fingered chelipeds with rudimentary ridges, the pilous elevations on the carapace are prominent in even the smallest males. The external surface of the major pollex has its upper and lower margins projecting, forming ridges.

*Affinities: U. inaequalis*, from the characteristics of its second maxilliped, major and minor chelipeds, orbital and suborbital regions, abdominal appendage of male and courtship display, definitely is a relatively primitive shoot on the branch giving rise to *U. oerstedi* on the one hand and to *U. batuenta* and *U. saltitanta* on the other. Its possession of a rudimentary stridulating apparatus, which is progressively better developed in the group of species terminating in *U. musica* and *U. terpsichores*, is interesting. The pilous elevations and relatively slight convexity easily distinguish it from its relatives.

*Material:* The 50 specimens were taken from Corinto, Nicaragua; from Puntarenas, Ballenas Bay, and Golfito, Costa Rica; and from La Boca, Balboa, Canal Zone. Cat. Nos. 381,139, 381,140, 381,141, 381,142, 4126.

### ***Uca tenuipedis*** sp. nov.

Text-figs. 4M, 5. Pl. II, Fig. 7; Pl. III, Fig. 13.

(See also pp. 149, 166, 169).

*Diagnosis:* Carapace strongly convex, but not quite semicylindrical in lateral view; front behind eyes about one-fourth maximum width of carapace; orbits little oblique; antero-lateral margins well developed, slanting outward, then continuing backward and inward with an angular turn; orbital angle usually about a right angle, sometimes slightly produced. Minor chelae strongly serrated or toothed in middle half, gape very slight, hairs plentiful on both outer and inner margins. Oblique tuberculated ridge inside major palm absent; pollex very broad basally. Merus of second maxilliped with about 15 to 25 spoon-tipped hairs. All segments of ambulatories unusually slender.

*Description:* A small species. Carapace with H-form depression shallow, regions poorly delimited; pile absent, but a sparse scattering of microscopic hairs over entire surface.

Carapace very convex, but not quite semicylindrical, widest behind orbital angles, at point where antero-lateral margins turn inward. These margins are straight, slanting outward, about two-thirds as long as width of front behind eyes. They then continue inward and backward with an angular turn in the form of the usual ridge as far back as posterior part of cardiac region. Sides of carapace faintly concave, little convergent. Front between posterior margins of eyestalks about one-fourth width of carapace, its margin invisible in dorsal view. Upper margin of orbit sinuous, not very oblique. Eyebrow extremely narrow, only about a quarter as wide as adjacent portion of eyestalk, strongly inclined. Lower orbital margin projecting, sparsely and irregularly crenulated in outer half; inner half entire. Suborbital region naked except for a row of hairs immediately behind crenulated margins. All abdominal segments distinct.

Spoon-tipped hairs on merus of second maxilliped numbering only about 15 to 25. Woolly hairs moderately plentiful. Ischium of third maxilliped with central grooves represented only by a marginal depression.

Minor chelae slightly longer than palm, with strong serrations or teeth throughout middle half; distal fourth slightly dilated, corneous, the tips articulating well. Gape very slight. An oblique row of hairs on inner surface of each chela, long and soft distally; another row of hairs, all moderately short, externally, and two other similar rows, along dorsal surface of dactyl and ventral surface of pollex, respectively.

Major cheliped of male with arm slightly rugose, wrist more so, both furnished with pile externally, the arm proximally, the wrist distally. Hand somewhat swollen, broad, about once and a fifth times as long as broad. Upper surface rounded, although there may be a row of fine granules; lower margin with a row of tubercles; upper and upper outer surfaces with fine sharp granules; the region is also faintly eroded; lower outer half of palm smooth.

Inner surface of large cheliped without an oblique tuberculated ridge, although there are sometimes one or two tubercles at the point where such a ridge usually meets the carpal cavity. Upper margin of carpal cavity bounded by a single row of minute, spinulous granules.

A row of well developed tubercles extends along proximal three-fourths of pollex, close to upper margin, and curves upward along distal part of manus, dying out below dorsal margin. No regular row of tubercles distal to this paralleling base of dactyl, although there may be three to five small tubercles in variable formation in this position; in the holotype four are clearly discernible, although they are very low; they are well separated and arranged in a slightly curving line. A sparse, irregular scattering of fine granules on upper half of inner surface of palm. Dactyl shorter than palm, finely tuberculated in upper proximal portion, curving downward beyond tip of pollex. Pollex roughly triangular, broader basally than dactyl, tapering abruptly along prehensile edge in distal two-fifths; tip produced slightly upward. Gape very slight; prehensile edges with low, blunt, similar teeth except for one which is slightly enlarged near base of dactyl, and another on pollex, at origin of the abrupt tapering. On external side of basal three-fifths of both dactyl and pollex, close to prehensile edge, is a row of tubercles; on pollex this row originates at lower part of dactyl's insertion, continuing around proximal end of gape, and so on out along pollex proper. A variable but small amount of pile and longer hairs is found on inner distal part of manus and proximal part of chelae, near prehensile edges.

All segments of ambulatories very slender in both sexes, the meri scarcely enlarged compared with those of other species. Merus of third ambulatory in male extending more than a quarter of its length beyond antero-lateral angle when laid forward; relatively shorter in female, though scarcely wider.

Abdominal appendage of male moderately slender, the distal half bending gradually forward, tapering slightly. Arm absent, represented only by a few bristles arising from a shelf slanting obliquely toward base of appendage, in its distal ninth.

*Measurements:* Male holotype; length, 5 mm.; breadth, 6.53 mm.; base of manus to tip of pollex, 8.1 mm. Larger female paratype: length, 5 mm.; breadth, 6.81 mm.; Largest male paratype; length, 5 mm. Smallest male paratype: length, 4.1 mm. Smaller female paratype: length, 4.5 mm. The largest of both sexes appear to be adult.

*Affinities:* This species is close to *U. inaequalis*, *U. batuenta* and their relatives. It is distinguished easily from all by the slender ambulatories and lack of an oblique tuberculated ridge inside of palm.

*Local Distribution:* The twelve specimens in the collection were all taken in mangrove mud at Ballenas Bay, Costa Rica.

*Material:* Male holotype; Cat. No. 381,143; nine male and two female paratypes, Cat. No. 381,144.

The name *tenuipedis* is given this species because of the slenderness of its legs.

***Uca batuenta*** sp. nov.

Text-figs. 4N, 5, 8; Pl. VI, Fig. 26.

(See also pp. 149, 153, 166, 169).

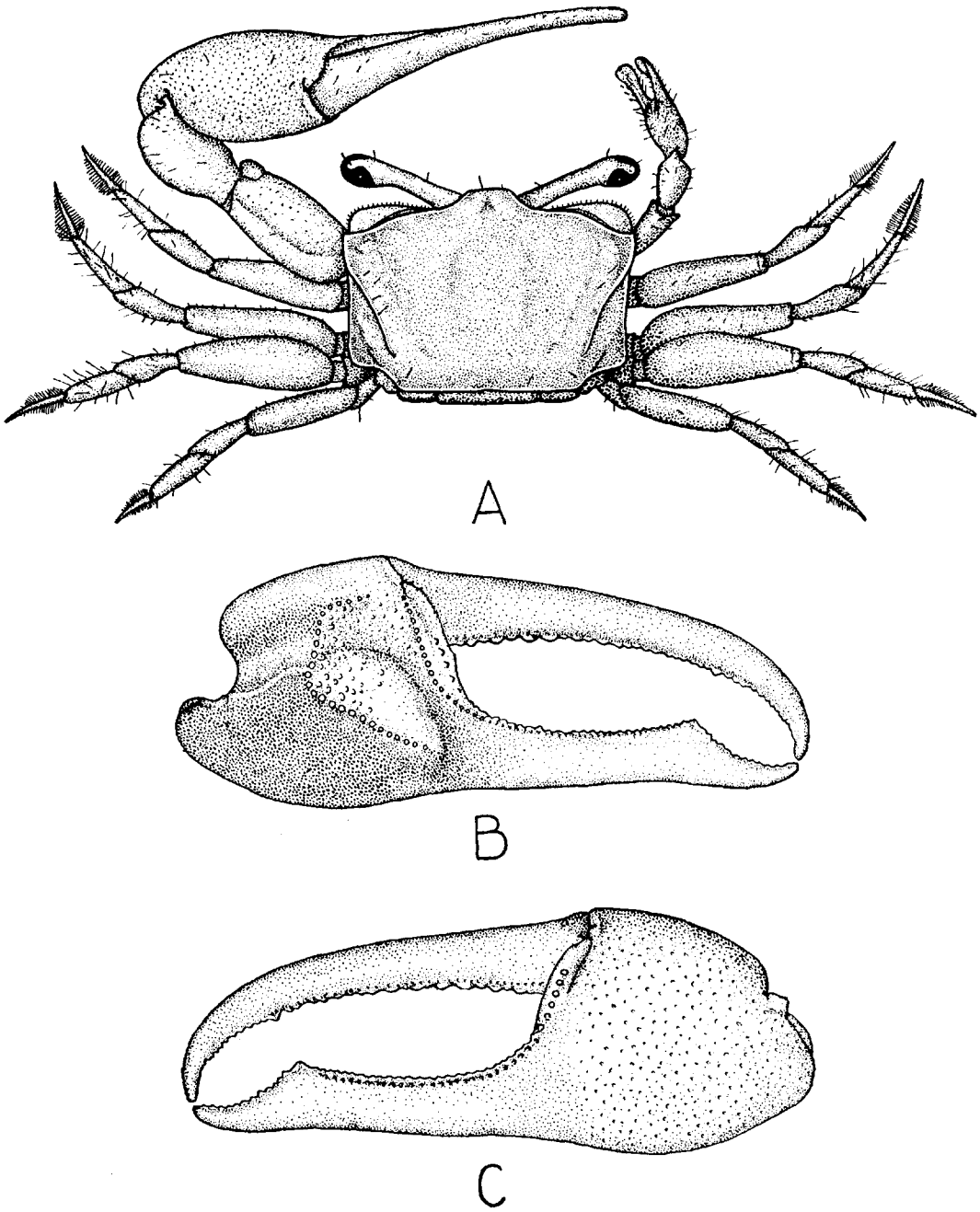
*Diagnosis:* Carapace strongly convex, practically semi-cylindrical in lateral view; front behind eyes a little more than one-fourth maximum width of carapace; orbits little oblique; antero-lateral margin well developed, straight or slanting a little outward, then curving backward and inward without forming a sharp angle; orbital angle a right angle, not produced. Minor chelae strongly serrated in middle half, gape very slight, hairs plentiful in rows on all margins. Oblique tuberculated ridge inside major palm present, continued to upper margin, but weak and irregular in upper portion; pollex moderately slender, not at all triangular, with an abrupt elevation on prehensile edge about three-fifths of way to tip; Merus of second maxilliped with only about a dozen or less spoon-tipped hairs. Merus of ambulatories slightly enlarged. No large, isolated teeth on outer edge of lower orbital margin. No arm on abdominal appendage of male. Eyebrow narrow.

*Description:* A small species. Carapace with H-form depression shallow, regions scarcely delimited, naked except for a very few widely scattered microscopic hairs.

Carapace strongly convex, practically semi-cylindrical in lateral view; widest at or behind orbital angles. Antero-lateral margins straight or slightly sinuous, usually slanting a little outward, about half as long as width of front behind eyes. They then curve gradually inward and backward, continuing in the form of the usual ridge as far as middle of cardiac region. Sides of carapace faintly concave, scarcely convergent. Front between posterior margins of eyestalks slightly more than one-fourth width of carapace, its margin invisible in dorsal view. Upper margin of orbit notably sinuous, scarcely oblique. Eyebrow very narrow, less than a third width of adjacent portion of eyestalk, strongly inclined. Lower orbital margin strongly projecting, entire, save for the occasional occurrence of several fine crenulations in extreme external corner. Suborbital region naked except for a row of hairs immediately behind orbital margin. All abdominal segments distinct.

Hairs with distinctly formed spoon-tips on merus of second maxilliped numbering a dozen or less; there may be a few more hairs with minute distal swellings. Woolly hairs relatively few in number. Ischium of third maxilliped with central groove represented only by a marginal depression.

Minor chelae slightly longer than palm, with strong teeth or serrations in middle half; distal fourth scarcely dilated, corneous, the tips articulating well. Gape slight basally, practically non-existent in serrated portions. An oblique row of hairs along inner surface of each chela, thick and long only distally; another row of hairs, all short and sparse, externally; three rows of short hairs along dorsal surface of dactyl, and two or three




Text-figure 8.

*Uca batuenta*, paratype. Length of carapace 4.2 mm. **A**, dorsal view; **B**, major cheliped, inner view; **C**, same, outer view.

along ventral side of pollex; the hair on these median rows are both short and moderately long.

Large cheliped of male with arm rugose only basally; rest of arm and wrist smooth, with a few fine hairs and, around carpo-manus joint, some short pile; long pile-like hairs inside base of arm. Hand broad, about once and a fifth or less times as long as broad. Upper surface with a low, ill-defined crest, dying out before reaching base of dactyl. Lower margin marked by a microscopically tuberculous, elevated line. A few minute tubercles scattered over outer surface, but these are so small and low that this area appears smooth to all intents and purposes; a very few short hairs are scattered over it.