

The Land Crabs of Costa Rica*

by

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(Received for publication August 5, 1966)

Some of the most interesting crustaceans in Costa Rica are the land crabs, members of the families Gecarcinidae and Coenobitidae. The major faunal list dealing with these forms was prepared by RATHBUN in 1918 (18). Other than distributional accounts (GARTH, 5, 6; HOLTHUIS, 9; RATHBUN, 19; and SCHMIDT, 21) this group has not been studied extensively in the field. Due to the intensive study in Costa Rica associated with the Organization for Tropical Studies at the University of Costa Rica, a more extensive knowledge of the local fauna has become imperative. Thus, the task has been undertaken to assemble previous information, supplement it by collecting, and prepare keys and species accounts.

METHODS

Field collecting was done along both coasts of Costa Rica (Fig. 1). The descriptions of habitat and the color given for each species are based solely on this work.

Because of the need for technical terms in constructing the keys, a glossary is included. Also there are sketches of the dorsal and ventral surfaces of a gecarcinid crab showing the major morphological features (Figs. 2 and 3).

In all instances the size data are for the largest individuals examined by the author. The length of the carapace for the gecarcinid crabs is measured along the median line (anterior to posterior). For the coenobitids, the carapace length is the distance from the tip of the rostrum to the posterior margin of the carapace located between the membranous lobes. Carapace width is measured at the widest point.

* Supported in part by NSF Grant No. GE 4705.

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DISCUSSION

In Costa Rica there are two families of land crabs: 1) the brachyuran family Gecarcinidae, represented by three genera containing six species; and 2) the anomuran family Coenobitidae, the land hermit crabs, represented by two species of the genus *Coenobita*. In each of these families there are closely related species, twin or geminate species, occurring on opposite coasts (Table 1). The resemblance between these species is much greater in some than in others. This pattern is a residual effect of the comparatively recent connection between the western Atlantic and Eastern Pacific oceans.

The Gecarcinidae have evolved a series of adaptations which make life successful on land. This success is directly related to their ability to adapt to the terrestrial environment through: 1) behavioral specialization such as specialized burrows, nocturnal activity, habitat preference and seclusion during ecdysis (see BLISS, 1, 2); and 2) physiological adjustments such as water conservation and storage, and osmotic controls (see EDNEY, 3 and GROSS, 7).

These crabs construct their burrows in areas adjacent to sources of water or in areas with soft and moist soil such as open fields, forest, and along the

TABLE 1

Geminate species occurring on opposite coasts of Costa Rica

<i>Pacific side</i>	<i>Atlantic side</i>
Gecarcinidae:	
<i>Gecarcinus quadratus*</i>	<i>Gecarcinus lateralis</i>
<i>Cardisoma crassum</i>	<i>Cardisoma quahumi</i>
<i>Ucides occidentalis</i>	<i>Ucides cordatus</i>
Coenobitidae:	
<i>Coenobita compressus</i>	<i>Coenobita clypeatus</i>

* This species also occurs on the Atlantic side just above the Isthmus of Panama.

margins of mangrove swamps. They have been found 30 kilometers from the shore and up to altitudes of 450 meters. These burrows represent an excavation of several feet in length and depth. Although no careful analysis has been made of burrow structure, they do provide protection from predators, a site for the storage of food, and as well a "home" with several advantages for conserving water, namely reduced temperature and increased humidity.

These crustaceans can exist in areas without a source of open water for several months. They must however, return to the sea for purposes of reproduction. They make an annual migration to the sea during April, May and June.

These movements are not inconspicuous. GARTH (5) gives the following account about *Cardisoma crassum* made by a member of the "Askoy" Expedition while in Panama:

"The land crabs range miles inland, but they all return annually to breed in their ancestral ocean home. The migration begins near the end of the dry season. In Panama this means the latter part of Lent, whence the tradition that the crabs are bent upon joining the Good Friday procession. Their pious motive does not deter the human population from capturing and eating vast numbers of them. At the time of the great marches, it is said that the world goes alive with crabs and that the forest floor sounds as though it were being whipped by hail."

Once they have arrived at the sea shore, copulation occurs and the eggs, which are attached to the abdominal appendages or pleopods, are shed into the water. By the time of shedding, the eggs have already developed to the zoeal stage. The males usually depart before the eggs are shed. After a few weeks, the young leave the sea and head up the shore toward the abode vacated earlier by the parents. These events take from four to six weeks. The newly fertilized eggs will be carried by the female until the following breeding period when they will have reached the zoeal stage of development.

The Coenobitidae are typically terrestrial in habit. Like the Gecarcinidae, they must return to the sea for the release of zoea. Observations on the larval development have been carried out in the laboratory (PROVENZANO, 16). The zoea are planktonic for a period, and then, after further development, they move out on shore and select a shell. Although they have been taken occupying a wide variety of gastropod shells, they are most frequently found in those of *Acanthina*, *Littorina*, *Nerita*, *Planaxis*, *Thais* and *Cerithium*. At first they can not tolerate long periods of exposure to dry air. But as they grow older the integument of the abdominal area becomes increasingly more calcified and thus more resistant to desiccation.

The adult coenobitids are found in the forest, open fields and on hills at great distances from the seashore. They may be directly exposed or under various types of vegetation.

Both the gecarcinids and coenobitids are scavengers. They feed on a wide variety of food items. Items found in stomach contents and observed being eaten include blue-green algae (*Calothrix* and others), fungi (*Daldinia concentrica*), coconut fragments, "old" crab shells or exuvia, beetles, and pieces of fresh and dried leaves from a number of trees such as the black mangrove (*Avicennia*), red mangrove (*Rhizophora*) and the figs (*Ficus*).

In almost any area where land crabs occur near the beach, one will encounter a variety of semi-terrestrial crabs. These will often be members of the family Ocypodidae, genus *Ocypode*. It is easy to confuse these crabs with some of the land crabs; however, a quick check of key morphological features will facilitate easy identification. These ocypodids are characterized by their pale yellow

colored carapace and legs as well as very pronounced eyestalks. Because of their color, they blend well with the moist sand or soil and are often almost invisible, thus their common name, the "ghost crabs". They abound along the shore where they construct shallow burrows. They are nocturnal, and at twilight time they are seen scampering over the sand in search of animal refuse which will serve as food.

GLOSSARY

ABDOMEN — posterior portion of the body, soft and coiled in the Coenobitidae, and hard and flexed beneath the carapace in the Gecarcinidae.

AMBULATORY LEGS — the second through fifth pereopods in the Gecarcinidae; the two pairs of appendages after the chelipeds in the Coenobitidae.

ANTENNAE — pair of jointed appendages located between the base of the eyes and the antennules in gecarcinids; located lateral to the eyes in the coenobitids.

ANTENNULES — pair of pointed appendages on either side of the median line.

ANTENNULAR CAVITIES — ventral depressions at the bases of the antennules.

BRACHIAL REGION — large lateral portion of the carapace posterior to the cervical groove.

CARAPACE — exoskeleton which covers the dorsal and ventro-lateral surface of the body in the Gecarcinidae; the chitinous shield covering the anterior portion of the body in the Coenobitidae.

CARDIAC REGION — median area of carapace, just above the heart, posterior to the cervical groove.

CERVICAL GROOVE — groove separating the anterior and posterior portions of the carapace.

CHELA — the claw; the last two segments of a cheliped.

CHELIPED — the appendage just posterior to the maxillipeds; it bears the chela.

COXA — the coxopodite; the first segment of a leg or maxilliped.

DACTYLUS — terminal or seventh segment of a maxilliped or walking leg; it is the movable part of the chela.

DISTAL — farthest from the center of the body.

EPISTOME — a ventrally located transverse plate forming the anterior border of the mouth cavity; it is fused to the carapace.

ENTIRE — a margin which is continuous and smooth, without conspicuous depressions or projections.

EXOGNATH — outer portion or branch (secondary one) of a maxilliped.

FINGERS — either the movable or nonmovable part of the chela.

- FLAGELLUM — terminal, segmented portion of the antenna or antennule.
- GONOPOD — first pleopod of male modified for the deposition of spermatophores.
- INTESTINAL REGION — a short transverse area just posterior to the cardiac region.
- INTERORBITAL AREA — the anterior margin of the carapace located between the orbits of the eyes.
- LAMINAR TEETH — series of triangular projections arranged in a linear fashion.
- MANUS — the palm or the hand; the modified propodus of the cheliped.
- MAXILLIPEDS — the three pairs of appendages modified as "jaw-feet"; the third pair form an operculum-like cover for the mouth cavity in the Gecarcinidae.
- MERUS — the fourth segment of a maxilliped or ambulatory leg.
- ORBITAL REGION — narrow area along the upper margin of the orbits of the eyes.
- PALP OF MAXILLIPED — the last two or three segments which extend from the merus of the maxilliped.
- PEDUNCLE — a stalk-like portion of an appendage.
- PEREIOPODS — the walking legs or ambulatory legs; includes the chelipeds.
- PLEPODS — the abdominal appendages; used in the female for carrying eggs; modified first pleopod in male is the gonopod.
- PROPODUS — the segment preceeding the dactylus.
- ROSTRUM — portion of the carapace projecting anteriorly between the bases of the eyes.
- SPINOUS — a series of spines either in a linear arrangement or arranged randomly along a given line.
- SUBEQUAL — almost equal.
- TELSON — the terminal segment of the abdomen.
- TUBERCLES — a series of smooth, knobby projections.
- ZOEA — larval stage with first six pairs of appendages functional and all trunk segment and lateral eyes present; characteristically the stage released from the egg by the land crabs.

SYSTEMATIC DISCUSSION

KEYS TO THE LAND CRABS OF COSTA RICA

A. KEY TO THE FAMILIES AND GENERA:

1. Abdomen reduced and tightly flexed beneath the thorax; distinct gap between the third maxillipeds (Family Gecarcinidae) 2

Abdomen extended, asymmetrical and well developed; chelipeds unequal, with left one much more pronounced; ambulatory legs of equal length or nearly so to larger of the chelipeds; antennular peduncles extremely long (Family Coenobitidae)

- *Coenobita*
 2 (1). Interorbital distance less than half of the greatest width of the carapace; exognath concealed or nearly so *Gecarcinus*

Interorbital distance more than half the greatest width of the carapace, exognath exposed

- 3
 3 (2). Anterior margin of merus emarginate, dactyli of legs spinous *Cardisoma*
 Merus quadrangular; dactyli of legs not spinous *Ucides*

B. KEY TO SPECIES OF THE GENUS *Coenobita*:

1. Oblique line of laminar teeth (Fig. 4-A) on the upper part of the outer surface of the left palm; pronounced projection on distal margin of left third pereopod (Fig. 4-B); ventral surface of dactylus of right third pereopod scoop-shaped (Fig. 4-C) *compressus*

No laminar teeth on upper part of outer surface of left palm (Fig. 4-D); lower distal surface of left third pereopod rounded and with pronounced serrations (Fig. 4-E); ventral surface of dactylus of right third pereopod not scoop-shaped (Fig. 4-F) *clypeatus*

C. KEY TO SPECIES OF THE GENUS *Gecarcinus*:

1. Merus of maxilliped with entire margin (Fig. 4-G); maxillipeds extend to epistome or nearly so; dactyli of legs with four rows of spines; chelipeds unequal *quadratus*

Merus of maxilliped with shallow rounded anterior emargination (Fig. 4-H); maxillipeds do not reach epistome; dactyli of legs with four rows of spines; chelipeds unequal in male *lateralis*

D. KEY TO SPECIES OF THE GENUS *Cardisoma*:

1. Male gonopod broad and blunt (Fig. 4-I); anterior and posterior margins of carapace strongly convex; legs sparsely hairy *quankumi*

Male gonopod flattened laterally, hairy, and with a long and slender spiral-like horny tip (Fig. 4-J); lateral margins of carapace with a ridge; legs conspicuously hairy *crassum*

E. KEY TO SPECIES OF THE GENUS *Ucides*:

1. Carapace slightly wider than long and without pronounced lateral margin or tubercles; dactyli six-sided with sharp granulated ridges *cordatus*

Carapace distinctly wider than long and with pronounced tuberculate lateral ridge; dactyli six-sided with smooth ridges *occidentalis*

Family COENOBITIDAE

Genus *Coenobita* Latreille 1826 (11)

Chelipeds unequal with the left one much more pronounced, the tips of fingers calcareous; ambulatory legs of equal length or nearly so to larger of chelipeds; carapace compressed anteriorly; rostrum absent; antennal peduncles compressed.

Coenobita compressus H. Milne Edwards 1837 (14)

Fig. 4-A, B, C.

COMMON NAME: Tropical land hermit crab.

RANGE: Agua Verde Bay, Lower California to Chile.

COLLECTING SITES: Bahía de Culebra, Playa del Coco, I. San Lucas and Golphito.

SIZE: Male 26.4 mm long; female 24.2 mm long.

HABITAT: Along the beach, margins of mangrove swamps, and in the forest; most abundant in areas which are devoid of dense undergrowth; mostly nocturnal.

COLOR: Left manus brown to brownish-orange; dactyli orange to yellow.

Coenobita clypeatus (Herbst) 1791 (8)

Fig. 4-D, E, F; Fig. 5

COMMON NAME: Tropical land hermit crab.

RANGE: Key Biscayne Florida to Venezuela including Bermuda, Bahamas and the West Indies.

COLLECTING SITES: Puerto Viejo, Guápiles, Moín, Portete and Cahuita.

SIZE: Male, 38.8 mm long; female, 30.3 mm long.

HABITAT: Along the seashore, in the forest and margins of mangrove swamps; often found a considerable distance from the ocean; nocturnal.

COLOR: Left manus a bright bluish-purple; adults with orange to yellow dactyli, young with grayish-blue dactyli.

Family GECARCINIDAE

Palp of external maxillipeds articulate either at the antero-external angle or at the middle of the anterior border of the merus; the exognath is slender and inconspicuous; the carapace is transversely oval with the antero-lateral borders strongly arched.

Genus *Gecarcinus* Leach 1814 (12)

Interorbital distance half or less than half of the greatest width of the carapace; orbits deep with eyes nearly filling the orbits; antennae very short; epistome linear; legs stout, the second pair being longest.

Gecarcinus quadratus Saussure 1853 (20)

Fig. 4-G

COMMON NAME: Red land crab.

RANGE: Acapulco, Mexico to La Libertad, Ecuador.

COLLECTING SITES: Bahía de Culebra, Cabo Blanco, Puntarenas, Boca de Barranca, Caldera, Pigres and Golfito.

SIZE: Male, 43.5 mm long, 56.0 mm wide; Female, 41.5 mm long, 52.0 mm wide.

HABITAT: Constructs burrows in forest and mangrove areas; frequently found among the roots of trees.

COLOR: Carapace brownish-red with two white spots in the cardiac region, intestinal region orange-red; large chelipeds light reddish-purple; merus of maxilliped light yellow; underside sooty white.

Gecarcinus lateralis (Fréminville) 1835 (4)

Fig. 4-H; Fig. 6

COMMON NAME: Black land crab; Common land crab.

RANGE: Bahamas, Florida to Macuto, Venezuela.

COLLECTING SITES: Moín, Portete and Cahuita.

SIZE: Male, 43.5 mm long, 58.0 mm wide; female, 48.0 mm long, 63.0 mm wide.

HABITAT: Dig deep burrows in soft sandy areas adjacent to the shore and in moist soil up to an altitude of 450 meters.

COLOR: Carapace dark red with small white spots justo posterior to the eyes and a pair of white spots in the cardiac region; chelipeds reddish-gray; dactyli sooty gray; underside cream-white.

Genus *Cardisoma* Latreille 1825 (10)

Interorbital distance much more than half the greatest width of the carapace; orbits deep, eyes filling half of the orbit; antennules folded; epistome short and well defined; legs stout.

Cardisoma quanbumi Latreille 1825 (10)

Fig. 4-I.

COMMON NAME: Great land crab; White land crab.

RANGE: Southern Florida to São Paulo, Brazil, including the West Indies.

COLLECTING SITES: Moín, Portete, Puerto Limón, Cahuita and Puerto Vargas.

SIZE: Male, 84.0 mm long, 106.0 mm wide; female, 59.0 mm long, 75.2 mm wide.

HABITAT: Open fields, margins of mangrove swamps, along margins of rivers and in forest; constructs deep and multi-chambered burrows.

COLOR: Carapace deep violet in young, but tends to become bluish-gray with age; ambulatory legs deep blue with larger cheliped dirty white.

Cardisoma crassum Smith 1870 (22)

Fig. 4-J; Fig. 7

COMMON NAME: Mouthless crab.

RANGE: La Paz, Lower California to Tumbes, Peru, and the Galápagos Islands.

COLLECTING SITES: Bahía de Culebra, Boca de Barranca, Playa del Coco and Golfito.

SIZE: Male, 105.0 mm long, 132.3 mm wide; Female, 61.0 mm long, 75.2 mm wide.

HABITAT: Open fields, margins of mangrove swamps, along roads and fences, and margin rivers and streams; constructs large, deep burrows, often with more than one entrance.

COLOR: Carapace deep blue; dactyli of legs red; large chela pale yellow to dirty white; underside cream-white.

Genus *Ucides* Rathbun 1897 (17)

Interorbital distance a little more than half the greatest width of the carapace; orbits deep but not much larger than the eyes; antennules oblique; epistome small and prominent; legs stout.

Ucides cordatus (Linnaeus) 1763 (13)

COMMON NAME: Pagurus; Wide red land crab.

RANGE: Southern Florida to Rio de Janeiro, Brazil including West Indies.

COLLECTING SITES: Portete, Cahuita and Puerto Vargas.

SIZE: Male, 72.3 mm long, 90.0 mm wide; female, 51.0 mm long, 61.3 mm wide.

HABITAT: Near sources of standing water, mangrove areas, and areas with underground seepage; digs moderately deep burrows.

COLOR: No field records; carapace bluish-black in alcohol.

Ucides occidentalis (Ortmann) 1897 (15)

Fig. 8

COMMON NAME: Wide red land crab.

RANGE: Espíritu Santo Island, Lower California to Las Vacas, Perú.

COLLECTING SITES: Playa del Coco, Puntarenas and Pigres.

SIZE: Male, 46.9 mm long, 65.9 mm wide; female, 51.5 mm long, 63.4 mm wide.

HABITAT: Mud of mangrove areas, mouths of rivers and adjacent to running water, open fields and along roads and fences where there is some standing water; burrows constructed in very soft mud and thus require constant repair.

COLOR: Carapace reddish-gray with orange-red on the lateral margins; last three ambulatory legs and most of chelipeds dark red; dactyli of chelipeds reddish-white; underside brownish-white.

ACKNOWLEDGMENTS

The author wishes to express his appreciation to Dr. Gerald Bakus of the University of Southern California for collecting several specimens from Cahuita, Costa Rica. He is indebted also to Dr. James McLean of the Los Angeles County Museum for having given him access to the collection there, and to Dr. John Garth of the Allan Hancock Foundation of the University of Southern California for his guidance and assistance.

SUMMARY

The land crabs of Costa Rica, members of the families Gecarcinidae and Coenobitidae, are described and keys are presented for their identification. A review of the recent literature is presented and also a brief discussion of the habits and life history of these land crabs. Species accounts include information on common name, range, collecting sites, size, habitat and color.

RESUMEN

En el presente trabajo se ofrece una descripción de los cangrejos terrestres de Costa Rica, miembros de las familias Gecarcinidae y Coenobitidae, y se dan las claves para su identificación. Incluye una revisión de la literatura reciente junto con una discusión de los hábitos de estos cangrejos terrestres. El estudio de las especies comprende información acerca del nombre vulgar, distribución, lugares de colección, tamaño, habitat y color.

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Fig. 1. Map of Costa Rica showing collecting sites of land crabs.

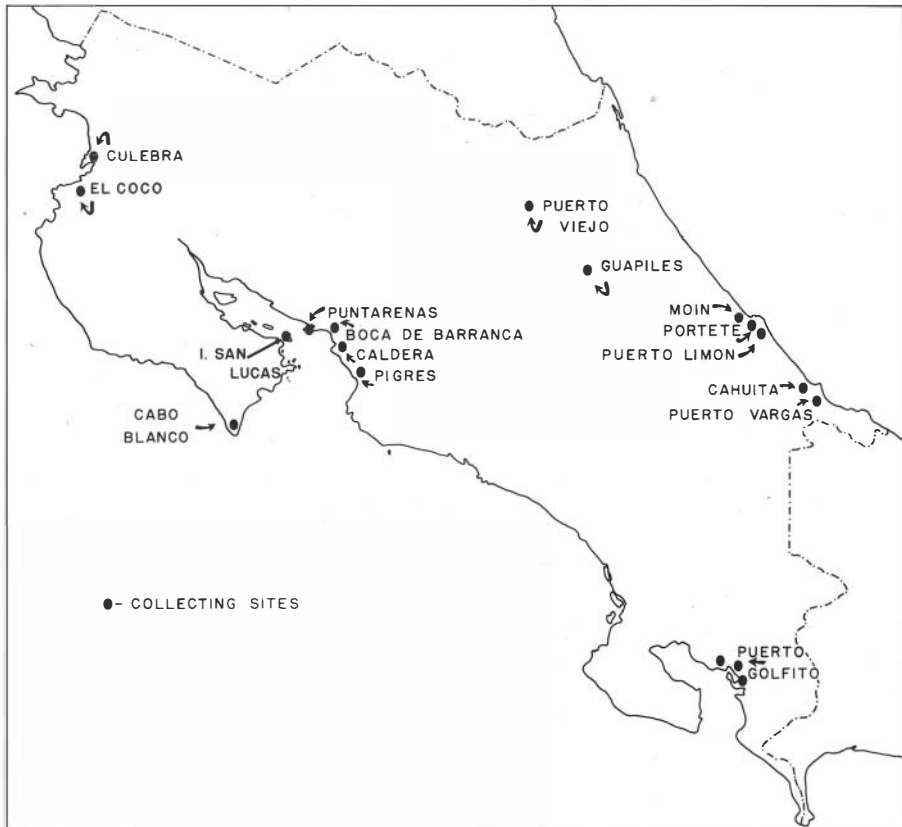
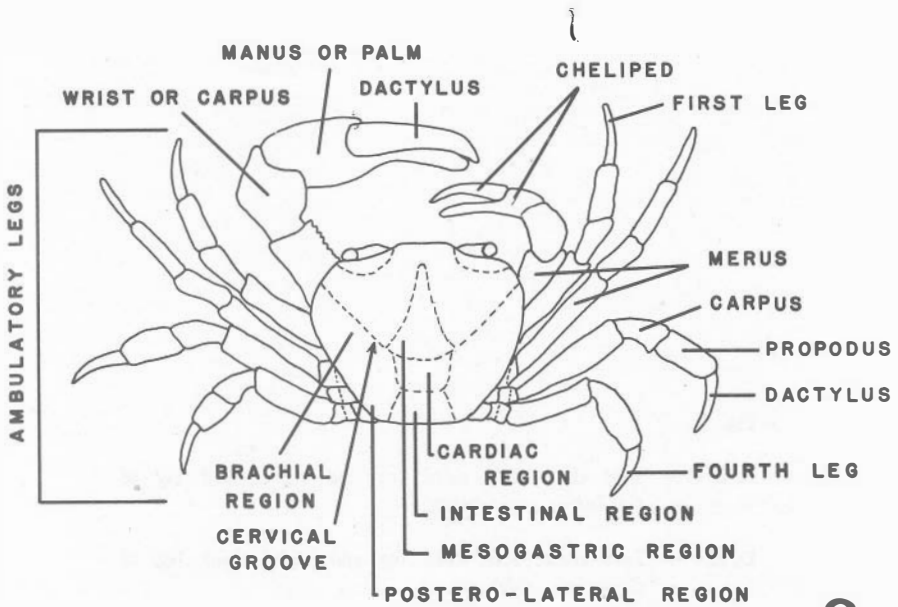
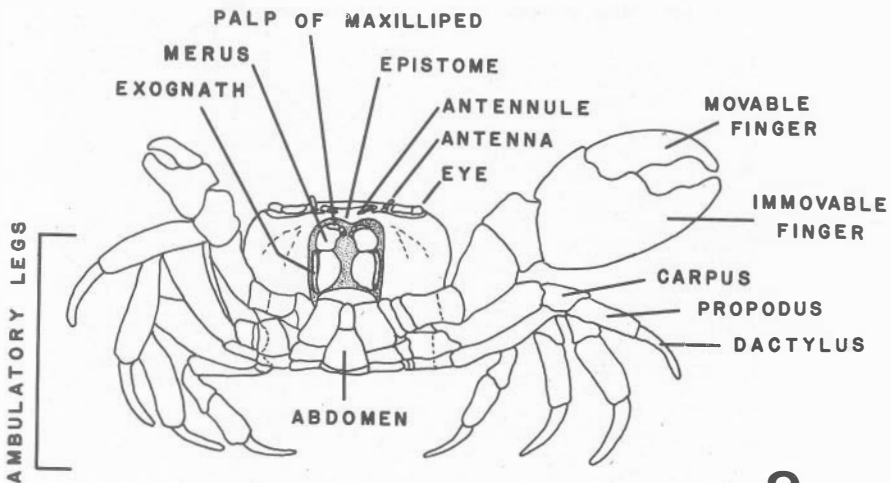


Fig. 2. Sketch of the dorsal surface of a gecarcinid crab showing the structures referred to in the discussion, keys and species accounts.

Fig. 3. Sketch of the dorsal surface of a gecarcinid crab showing the structures referred to in the discussion, keys and species accounts.



2



3

Fig. 4.

A, B, C — Left chela, left third leg and right third leg of
Coenobita compressus.

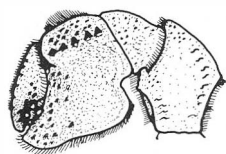
D, E, F — Left chela, left third leg and right third leg of
Coenobita clypeatus.

G — Third maxilliped of *Gecarcinus quadratus*.

H — Third maxilliped of *Gecarcinus lateralis*.

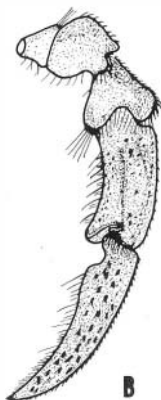
I — Male gonopod of *Cardisoma quahumi*.

J — Male gonopod of *Cardisoma crassum*.



A

10 MM.



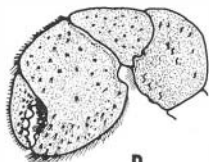
B

10 MM.



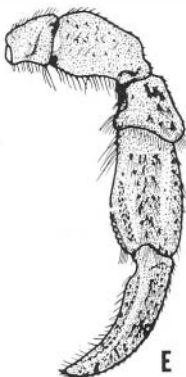
C

10 MM.



D

10 MM.



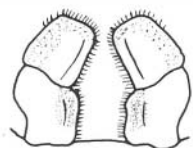
E

10 MM.



F

10 MM.



G

10 MM.



I

5 MM.



H

10 MM.

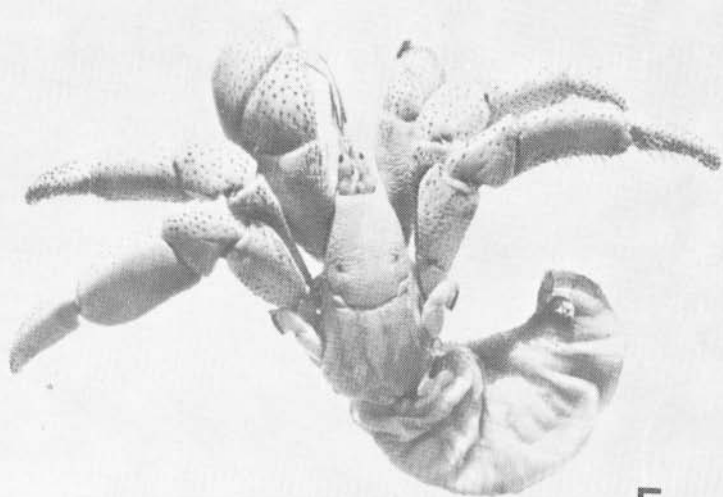


J

5 MM.

Fig. 5. *Coenobita clypeatus*, dorsal view, male, carapace 33.8 mm long.

Fig. 6. *Gecarcinus lateralis*, dorsal view, female, carapace 28.6 mm. long and 34.0 mm wide.



5



6

Fig. 7. *Cardisoma crassum*, dorsal view, male, caparace 49.2 mm. long and 60.4 mm wide.

Fig. 8. *Ucides occidentalis*, dorsal view, male, caparace 46.9 mm long and 65.9 mm wide.

