

Figure 17.-Callinectes sapidus Rathbun, forma acutidens: a, chelae in frontal view; b, carapace; $\mathbf{c}$, abdomen and sternal area, male, USNM 18630, Río Escondido, Nicaragua; d, abdomen and sternal area, female, USNM 99848, Roca Arroyo Balizas [= Arroyo de Valizes?], Uruguay; $\mathbf{a} \times 0.9$; $\mathbf{b}, \mathbf{c} \times 1$; $\mathbf{d} \times 1.1$.

Figure 18.-Male, first gonopods in situ with abdomen removed; portions of thoracic sternites IV-VIII: a, Callinectes marginatus (A. Milne Edwards), USNM 72351, Salt River Bay, St. Croix, V.I.; b, C. similis Williams, paratype, UNC-IMS 1556, Beaufort Inlet, Carteret County, N.C.; c, C. gladiator Benedict, Côte du Dahomey, $6^{\circ} 19^{\prime} \mathrm{N}$, $2^{\circ} 24^{\prime}$ E; d, C. ornatus Ordway, USNM 48401, Punta [ $=$ Cabo] Cajón, Cuba; e, C. danae Smith, USNM 60983, São Francisco, Niterói, Estado de Rio de Janeiro, Brazil; f, C. arcuatus Ordway, USNM 33417, Isla Magdalena, Baja California, Mexico; g, C. exasperatus (Gerstaecker), UNMIMS 2137, Bahía Fosforescente, P.R.; h, C. bellicosus (Stimpson), USNM 15436, La Paz Harbor, Baja California, Mexico; i, C. toxotes Ordway, USNM 18507, Acapulco, Guerrero, Mexico; j, C. bocourti A. Milne Edwards, USNM 72354, Fairplain stream above bridge, St. Croix, V.I. Scales = 1 cm ; a-f have higher magnification.








 Scales $=1 \mathrm{~mm}$; a-c have higher magnification.

Figure 21.-Callinectes sapidus Rathbun, male, right first gonopod, distal portion in posterior view unless otherwise indicated: a, typical form, USNM 41457, Hudson River at West Point, N.Y.; b, typical form, USNM 92452, Wye River, Chesapeake Bay, Md.; c, d, typical form, USNM 60601, Cape Hatteras, N.C.; e, acutidens form, USNM 122944, Deep Lake, Miami, Fla; f, typical form, right first gonopod, USNM 7679, Jamaica; g, acutidens form, USNM 72356, Fairplain stream below bridge, St. Croix, vuela; k, typical form, USNM 80650, Lago de Maracaibo, Venezuela; l, same specimen, right side; m, acutidens form, holotype, MCZ 4696 , Santa Cruz, Estado de Bahia, Brazil;
 (tip straightened in preservation). Scales $=1 \mathrm{~mm} ; \mathbf{a}, \mathbf{g}, \mathbf{n}$ have higher magnification.


Figure 22.-Female, left gonopore and portions of thoracic sternites IV-VII: a, Callinectes similis Williams, paratype, UNC-IMS 1556, Beaufort inlet, Carteret County, N.C.; b, C. marginatus (A. Milne Edwards), USNM 73285, W end San Juan I. near Ft. Gerónimo, P.R.; c, C. gladiator Benedict, Coast of Cameroon, $3^{\circ} 32^{\prime}$ N, $9^{\circ} 35^{\prime}$ E; d, C. ornatus Ordway, USNM 7584, Curaçao; e, C. danae Smith, USNM 60983, Sāo Francisco, Niterói, Estado de Rio de Janeiro, Brazil; f, C. arcuatus Ordway, USNM 15431, Estero de los Algodones near Guaymas, Sonora, Mexico; g, C. exasperatus (Gerstaecker), USNM 24467, Puerto Real, P.R.; h, C. bellicosus (Stimpson), USNM 60010, Pt. Abreojos, Bahía Ballenas, Baja California, Mexico; i, C. toxotes Ordway, USNM 18507, Acapulco, Guerrero, Mexico; j, C. bocourti A. Milne Edwards, USNM 18235, Sabanilla, Colombia; k, C. rathbunae Contreras, USNM 122922, Laguna de Alvarado, Veracruz, Mexico; 1, C. maracaiboensis Taissoun, paratype, USNM 139621, Lago de Maracaibo, Venezuela. Scales $=1 \mathrm{~mm}$.

WILLIAMS: CRABS OF THE GENUS CALLINECTES



Figure 23.-Female, left gonopore and portion of thoracic sternites IV.VII: a, Callinectes latimanus Rathbun, Plage de Pointe Noire, Congo; b, C. sapidus Rathbun, typical form, USNM 30567, Cameron, La.; c, C. sapidus Rathbun, acutidens form, USNM 99848, Roca Arroyo Balizas [ = Arroyo de Valizes?], Uruguay. Scales $=1 \mathrm{~mm}$.

Measurements of elements in the broad apronshaped abdomen of sexually mature females included:
13. Greatest width of segment 2 .
14. Greatest width of segment 3 .
15. Greatest width of segment 5 .
16. Median length of segment 5 .
17. Greatest width of segment 6 .
18. Median length of segment 6.
19. Median length of segment 3 (proximal edge) to tip of telson.
20.* Length of telson.
21.* Width of telson.

Analysis of selected nonsexual characters.Study showed that some of these measurements were more valuable than others at the specific level and 11 (marked with asterisks), generally considered useful in verbal description, were chosen for cluster analysis. Unfortunately, they neither clustered as species nor as species groups when analyzed. Results indicated that specific morphological differences in this genus are based on characters other than, or in addition to, those measured and analyzed in this test. Measure-
ments therefore were judged to have limited value in identification.

This finding is supported strongly by evidence other than results of the attempt at cluster analysis. Female Callinectes attain sexual maturity in a terminal metamorphic molt. Males attain an adult conformation at sexual maturity but may continue to molt at reduced frequency. Van Engel (1958) and others have shown that C. sapidus females molt 18 to 20 times in attaining maturity, males 18 or 19 before becoming mature and 3 or 4 times beyond that stage. The range of variation in number of molts may be much greater than this, for both dwarf and giant sexually mature individuals are known. Allometric changes accentuated at the two ends of this continuum attest to wide variability in form. Estévez (1972) emphasized variability in C. arcuatus and C. toxotes. Tables 1 and 2 show means, standard deviation, and sample size for selected characters from adult male and female Callinectes species. For almost all species the coefficient of variation ( $V=100 \mathrm{~s} / x$ ) is high for all characters shown, an indication that morphometrically there is great variation in the group. Simpson, Roe, and Lewontin (1960:91) stated that $V$ values greater than 10


Figure 24.-Respective geographic distributions of Callinectes arcuatus Ordway, C. danae Smith, C. gladiator Benedict, and C. similis Williams in the Atlantic and eastern Pacific oceans based on specimens studied and verified published records.
indicate that a sample is not reasonably unified. Throughout the genus great variation in morphometry of the body makes keys for identification involving proportions almost impossible to devise unless qualified by exceptions.

From a different viewpoint, Stephenson et al. (1968) applied methods of numerical analysis to 44 species and putative subspecies of Portunus (mainly from America, but certain Indo-Pacific species for comparison), Callinectes, Arenaeus, and Scylla, relying on presence or absence of 57 characters to build up a data matrix from which character assessments could be made. The method nicely demonstrates that Callinectes is a very homogeneous group, but the internal relationships implied do not correspond harmoniously with classical interpretation. This is not a matter of conflict, but simply one of judgment, the method seeming to be limited by interpretation of charac-
ter states, weighting being one serious problem and choice of characters another. Were the analysis run with different emphases, results might reflect those to some extent.

## LARVAL DEVELOPMENT

Among Callinectes species, larval development of only C. sapidus and C. similis has been determined by hatching eggs and rearing in the laboratory. Costlow, Rees, and Bookhout (1959) and Costlow and Bookhout (1959) described seven zoeal stages, atypically an eighth, and a megalopa for C. sapidus. Larvae and megalopae of the two species are apparently almost identical, the stages being similar to those of other portunids (Costlow and Bookhout, pers. commun.). Importantly, the megalopae of Callinectes lack an internal carpal spine on the chelipeds whereas megalopae of Portunus have a well-developed spine on this member


Figure 25.-Geographic distribution of Callinectes ornatus Ordway in the western Atlantic Ocean based on specimens studied and verified published records.


Figure 26.-Respective geographic distributions of Callinectes exasperatus (Gerstaecker) and C. sapidus Rathbun in the western Atlantic Ocean with introductions to the eastern Atlantic and Mediterranean Sea, based on specimens studied and verified published records.
(Williams, 1971), showing one of the generic distinctions at an early phase of development.

Costlow ( 1965,1967 ) followed the early work on larvae with a series of experimental studies showing that development of $C$. sapidus is subject to variation both in staging and duration. Total development time of C. sapidus from hatching of egg to transformation of the megalopa to first crab stage has varied from 31 to 69 days in the laboratory in various combinations of salinity and temperature, but duration of individual stages is variable even in a single salinity-temperature combination. The stages are constant enough, however, that Van Engel (1958), Cargo (1960), Nichols and Keney (1963), Pinschmidt (1964), Tagatz (1968), More (1969), and Williams (1971) were able to identify zoeae or megalopae from nearshore oceanic and estuarine plankton. In nature as in experiments, development time may be extended
by environmental conditions. Megalopae have been found throughout the year in North Carolina estuaries.

## FOSSIL RECORD

Hard parts of portunids most abundant as fossils in Tertiary formations in eastern North and Middle America are portions of the chelipeds, usually the dactyls and portions of the propodi. Some deposits contain remains of carapaces and/or sterna, occasionally almost whole exoskeletons of crabs, but any of the remains are scarce. It was largely on the basis of cheliped fragments that Rathbun (1919a, b, 1926, 1935) listed and described Callinectes species from formations attributed to ages as old as the Oligocene. Withers (1924) described a fragment of chela from the Eocene of Jamaica as Callinectes, and Blake (1953) added information


Figure 27.--Respective geographic distributions of Callinectes bellicosus Stimpson, C. bocourti A. Milne Edwards, C. latimanus Rathbun, C. marginatus (A. Milne Edwards), C. maracaiboensis Taissoun, C. rathbunae Contreras, and C. toxotes Ordway in the Atlantic and eastern Pacific oceans based on specimens studied and verified published records.
on remains from the Quarternary. Williams (1965) uncritically accepted determinations for Atlantic and Gulf Coastal Plain records from the Miocene to Recent, but study of this material, even though its interpretation is beyond the scope of the present paper, leads to an attitude of restraint.
The characters by which Callinectes is distinguished from other portunid genera, shape of male abdomen and lack of an internal carpal spine on the chelipeds, are rarely evident in the fossil material, the only undoubted specimens (treated in species accounts below) coming mainly from Pleistocene and a few Miocene horizons. All others studied lack characters for positive first order identification and therefore their determinations rest on secondary features such as shape of the chelae or other nondiagnostic parts of the body. Although the numerous cheliped fragments most resemble these parts in living species of Cal-
linectes, they also resemble those of Ovalipes and certain Portunus, especially the large $P$. pelagicus and $P$. sanguinolentus distributed widely in the Indo-Pacific region today (Stephenson, 1962), as well as the robust Arenaeus cribrarius and $A$. mexicana, respectively from Atlantic and Pacific shores of the Western Hemisphere (Rathbun, 1930). A single propodal finger of a form attributed to $P$. sayi reported from the Miocene of Florida (Rathbun, 1935) greatly resembles other remains attributed to Callinectes. Margins of warmer seas of early and mid Tertiary (Ekman, 1953; Hazel, 1971) could have favored such forms or others like contemporary Scylla of Indo-Pacific waters, fossil representatives of which were described [ $=$ ?] by Rathbun (1919b, 1935) from the Miocene of Florida, Dominican Republic, and Mexico. Judging by ecological requirements of living species, Callinectes would have been well
adapted to such an environment, but fossil evidence for its existence in the Paleocene remains indirect.
There are constant structural differences between the early fossil series and modern Callinectes. The palms of chelae of C. jamaicensis Withers, 1924 (Eocene), C. alabamensis Rathbun, 1935 (Oligocene), C. declivis Rathbun, 1919a (lower Miocene), and C. reticulatus Rathbun, 1919a (Oligocene-lower Miocene) are short and faceted more like Callinectes than other living genera of portunids, but they are relatively thinner than in living members of the genus. The fingers in these early forms have length-width proportions and tooth arrangements that resemble modern $C$. sapidus, but the tooth rows are relatively narrower proximally on propodal fingers and less inclined toward development of a molariform crushing surface. Of the four external facets on the palm, the upper mesial one in the fossil series is always inclined downward toward the inner surface in major chelae whereas in modern Callinectes species it is nearly horizontal in the major chela and noticeably inclined downward only in the minor one; moreover, the third or dorsolateral facet is relatively wider in living Callinectes species than in any of the early fossils. Compression and erosion may have altered relief but not uniform angle of inclination of facets in the fossils. Generally, fossils older than early-mid Miocene attributed to Callinectes have less powerful chelae than living species and these differences in structure seem significant enough to warrant generic separation of the two series when more material comes to light.

## MODERN DISTRIBUTION

Confined almost exclusively to shallow, often brackish coastal waters as adults, the genus Callinectes is represented by six species distributed (Figures 24-27) around the Caribbean Sea and southward to southern Brazil: C. marginatus, ornatus, danae, exasperatus, bocourti, and sapidus. A seventh species, C. maracaiboensis, is localized in estuaries of Venezuela. One of these species, $C$. marginatus, bridges the Atlantic, ranging with $C$. gladiator and C. latimanus from Mauritania to Angola in West Africa. It also reaches the Cape Verde Islands. Only three species occur in the Gulf of Mexico, exclusive of the southeastern part off Florida: $C$. rathbunae, an isolated relative of $C$. bocourti in the western Gulf, C. similis, an essen-
tially Carolinian form ranging northward along the coast, and C. sapidus, which ranges far beyond, occasionally to the Maritime Provinces of Canada. In the eastern Pacific, disregarding distant island occurrences, C. arcuatus is distributed from extreme southern California to Peru, sharing its range with C. bellicosus in the region of Baja California and with C. toxotes from there south.
If one relies on structure of male first gonopods alone for estimation of morphological similarity, the following zoogeographical associations emerge. The set of species with short first gonopods (C. marginatus, gladiator, ornatus, and similis) has separate eastern and western Atlantic components, and one member on both sides of the tropical Atlantic. The second set with longer first gonopods (C. arcuatus, bellicosus, danae, and exasperatus) occurs in the tropical western Atlantic and eastern Pacific. The third set with quite long first gonopods (C. toxotes, bocourti, rathbunae, maracaiboensis, latimanus, and sapidus) has representatives in all regions. Distributions of all species fit patterns accepted by Ekman (1953:30, ff.) as representative of many along the tropical-subtropical Atlantic and east Pacific coasts, but one, C. sapidus, has a latitudinal range that seems to exceed this pattern. In this species, development of a northern and southern form may be in progress.

The amphi-Atlantic distribution of C. marginatus, records of C. exasperatus, marginatus, ornatus, and sapidus from Bermuda, C. arcuatus from the Galápagos Islands, C. toxotes from Juan Fernández, as well as less removed northern marginal records for essentially southern species along the North American continent (C. bocourti in southern Florida and Mississippi; C. marginatus in North Carolina; C. similis in New Jersey; C. sapidus in Nova Scotia) all point to extensions of range by larval transport in currents (Verrill, 1908b; Garth, 1966). Investigators working with larval stages (reviewed in Williams, 1971) suggest that larvae and megalopae can move considerable distances; zoeae have been found off St. Johns River, Fla., at stations up to 160 km , and megalopae in the same area up to 128 km from shore. In Chesapeake Bay and Pamlico Sound, N.C., megalopae have been found 170 and 100 km respectively from presumed points of entry to the estuarine systems. Most of this off-and-onshore movement of larval stages appears to be a homeostatic developmental feature in the life
histories of the species. Among spiny lobsters, whose larvae are seemingly better fitted for temporary pelagic existence than crab larvae because of leaflike shape, up to 6 mo or greater duration of larval life occurs (Lewis, 1951; Austin, 1972). Phyllosomas of some spiny lobsters are rarely found beyond the latitudinal geographic limits of the coastal adult population. George and Main (1967) attributed this result to behavioral responses of the larvae, vertical migration, etc., within prevailing current systems which act to preserve integrity of distribution, but Austin (1972) held open the idea of long distance transport over considerable lengths of time. Some dispersal of larvae at the fringes of less pelagic Callinectes populations obviously occurs, but the wanderers are at a competitive disadvantage in establishing temporary range extensions. Nevertheless, larval dispersal of Callinectes coupled with movement of adults, judged to be minor except within an estuarine system (Fischler and Walburg, 1962; Tagatz, 1968), seems to assure genetic continuity over broad areas.

If one accepts the tenet that the center of evolution for a group contains the largest number of species, Neotropical Atlantic American shores seem to be the primary center in which the genus Callinectes developed and from which it radiated. Fossil evidence indicates that this radiation took place in the Tertiary, a period of time in which land-water relationships of that region diverged widely from their positional and areal extent today (Woodring, 1966, 1971). Olsson (1972) regarded the Miocene as the time when Panamanian molluscan biotas related to those of today evolved under conditions of general subsidence and when parts of present day Central America were reduced to an archipelago of large islands separated by straits between the Caribbean and east Pacific. Ekman (1953), Fell (1967), and others regarded the marine fauna that evolved in this region as an impoverished western outpost of the Tethyan fauna, related most closely to that of the eastern Atlantic and southern Europe. Though the tropical Atlantic and neighboring east Pacific regions both shared in the radiation of Callinectes, the conservatism of this offshoot contrasts remarkably with the far richer divergence of its parent stock. Stephenson (1962) considered the Indo-Pacific, with 175 living species, as the germinal center for the Portunidae. It seems reasonable to view Callinectes as a portunid group evolving at the geographic limits of the family,
specializing in occupation of estuaries, and paralleling in many ways the heavy-bodied IndoPacific Scylla serrata (Stephenson, 1962)

If Callinectes evolved mainly in the Caribbean faunal province, the present distribution of species in essentially three isolated centers raises questions concerning dispersal. Separation of the east Pacific from the Caribbean by elevation of the Panamanian isthmus near the close of the Tertiary understandably isolated certain elements of the genus and may have promoted further radiation, but close relationship of species in the two areas is emphasized by an obvious geminate pair -danae-arcuatus-similar in a number of morphological features, which occurs today on east and west coasts of Middle and South America. Separation of the east and west Atlantic fragments of the genus is harder to resolve because not only does one species bridge this gap, but two species groups (short and long first gonopods) are represented on both sides of the ocean, seemingly specialized along the same general lines. Which is the ancestral stock? Were pelagic larvae the mechanism of transport, as Fell (1967) proposed for analogous but cold-tolerant echinoderms, perhaps aided by island stepping stones in the mid Atlantic? (Fell rejected continental drift as a plausible explanation for transport, an idea more acceptable today than it was in 1967, but involving a time span greater than concerned here [McKenzie, 1972].) Length of life of the larvae of most species of Callinectes under pelagic conditions remains unknown. West Africa is upstream from the Western Hemisphere in prevailing equatorial surface currents. It seems unlikely that the larvae could move counter to this current from a center in the west or survive the much longer (and today, colder) northern transit from the West Indies via the Gulf Stream beyond Bermuda to the Azores, Canaries, and finally to west Africa. So far as known, all Callinectes utilize estuaries during part of their lives. Populations on small islands may be nonbreeding, transitory implants, or unsuccessful breeders. Means and paths of longdistance transport, and effectiveness of transients in colonization, among these forms will remain unknown until more data are collected.
Finally, the clustering of species by numerical methods employed by Stephenson et al. (1968) does not reflect the three groups suggested by first gonopod types, but it does support classical interpretation setting $C$. marginatus and perhaps $C$. gladiator aside as the most peripheral morpholog-
ically. It suggests that the three west American species, C. arcuatus, bellicosus, and toxotes differ appreciably from each other and that they arose from eastern American ancestors. It also supports the idea that most of the postulated "centra" species occur in the Atlantic and that "it is conceivable that the group originated from an eastern American ancestor." Beyond this the results are less compatible with conclusions reached here, but the analysis was done without including C. similis which may be a linking form that would have changed the interpretation.

## SPECIES ACCOUNTS

In the species accounts that follow, the synonymies include only citations of works that primarily are concerned with descriptive, taxonomic, or zoogeographic information. The reason for this limitation is that commercially valuable species often have a voluminous literature. All inclusive synonymies for them become so unwieldy that the real purpose-taxonomic history of the species-becomes obscured. The descriptions also are limited because full descriptions are elsewhere in the literature.
Two features included in the descriptions need clarification. The term "metagastric area" is employed for the central trapezoidal area of the carapace in the sense Chace and Hobbs (1969) used it rather than the term "intramedial area" employed by others (cf. Rathbun, 1930; Williams, 1966). Strictly speaking, this region of the carapace includes the undifferentiated metagastric (over $90 \%$ ) and at least part of the shortened urogastric (less than $10 \%$ ) areas, but for all practical purposes the first term is sufficiently explicit. The number of anterolateral teeth in Callinectes is nine (Rathbun, 1930), but the first of the series is also known as the outer orbital tooth and the last as the lateral spine. This partition of the series is observed here. The first and last teeth are always named and the small teeth are numbered.
Abbreviations adopted for institutions loaning study material are: AHF, Allan Hancock Foundation, University of Southern California; AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences of Philadelphia; BMNH, British Museum (Natural History), London; MCZ, Museum of Comparative Zoology, Harvard; MNB, Museu Nacional, Rio de Janeiro; MNHNP, Museum National d'Histoire Naturelle, Paris; RMNH, Rijksmuseum van Natuurlijke

Historie, Leiden; SADZ-B, Secretaria da Agricultura, Departamento Zoologia, São Paulo; UNCIMS, University of North Carolina, Institute of Marine Sciences, Morehead City; USNM, National Museum of Natural History, Washington, D.C.; YPM, Peabody Museum of Natural History, Yale University, New Haven, Conn.

Supplementary literature records are occurrences not represented by specimens studied, but accepted on basis of supporting data.

## GENUS CALLINECTES STIMPSON, 1860

Callinectes Stimpson, 1860, p. 220 [92].- Rathbun, 1896, p. 349 (revision).- 1921, p. 394 (review of African species).- 1930, p. 98 (review of Western Hemisphere species).- not Chen, 1933, p. 95 (=Portunus?).- Monod, 1956, p. 204 (review of African species).- Garth and Stephenson, 1966, p. 42 (review of eastern Pacific species).

Description.-Portunid crabs lacking an internal spine on carpus of chelipeds. Abdomen of males broad proximally, narrow distally, roughly T-shaped; first segment broad, almost hidden; second segment broad, slightly overlapping coxae of fifth pereopods at each side; third-fifth segments fused and tapering sinuously from broad third to distally narrow fifth; sixth segment elongate and narrow; telson ovate with acute tip. Abdomen of females exhibiting two forms: immature females with abdomen triangular from fourth segment to tip of telson, segments fused; mature females with abdomen broadly ovate (excluding telson), segments freely articulated; first segment almost hidden; second and third segments slightly overlapping coxae of fifth pereopods at each side; fifth and sixth segments with greatest sagittal length; sixth segment narrowing distally in irregular broad arc to articulate with triangular telson. Abdomen and telson of both sexes reaching anteriorly beyond suture between thoracic sternites IV and V.

Type species.-Callinectes sapidus Rathbun, 1896, by designation of International Commission of Zoological Nomenclature (1964:336).

Gender.-Masculine.
Number of species.-Fourteen, which may be distinguished by the following keys.

## KEY TO SPECIES OF CALLINECTES (EXCLUDING JUVENILES)

Figures 3-17

1. Front with two prominent, broad based, triangular teeth between inner orbitals; each with or without rudimentary submesial tooth on mesial slope (Atlantic; Western Hemisphere, introduced in Europe) ..... sapidus.
$1^{\prime}$. Front with four teeth between inner orbitals, or two prominent lobulate or narrowly triangular teeth separated by a nearly plane space often bearing a pair of rudimentary submesial teeth ..... 2
2. Submesial pair of frontal teeth well developed and more than half as long as lateral pair (measuring from base of lateral notch between teeth) ..... 3
$2^{\prime}$. Frontal teeth decidedly unequal in size, submesial pair no more than half as long as lateral pair (measuring from base of lateral notch between teeth), or vestigial ..... 8
3. Four frontal teeth reaching nearly common level ..... 4
$3^{\prime}$. Submesial frontal teeth definitely falling short of lateral pair ..... 7
4. Four frontal teeth lobulate, not triangular (Pacific; Baja California-Juan Fernández) ..... toxotes.
$4^{\prime}$. One or both pairs of frontal teeth triangular ..... 5
5. Four frontal teeth with rather rounded tips, lateral pair more broadly triangular than submesial pair and with mesial side having more oblique slope than lateral side ..... 6
$5^{\prime}$. Four frontal teeth acute, lateral pair usually broader than submesial pair (Atlantic; Mexican Gulf coast) rathbunae.
6. Anterolateral teeth trending forward, their anterior margins shorter than posterior; vestiges of reddish color usually persisting in preserved specimens (except long- preserved ones); distal border of sixth abdominal segment in mature females broadly triangular (Atlantic; Caribbean-South America) bocourti.
6'. Anterolateral teeth directed outward, their tips acuminate and margins shouldered at least in anterior portion of row; vestiges of greenish color usually persisting in preserved specimens (except in long-preserved ones); distal border of sixth abdominal segment in mature females semiellipsoid (Atlantic; Venezuelan estuaries) . . . maracaiboensis.
7. Granules on ridges and crests of chelae coarse and well separated (Atlantic; Caribbean- South America) ..... exasperatus.
$7^{\prime}$. Granules on ridges and crests of chelae moderate to fine and closely crowded, often worn smooth in adults (Atlantic; West Africa) latimanus.
8. Carapace remarkably smooth, lines of granules visible but barely perceptible to touch (except epibranchial line variably prominent) ..... 9
$8^{\prime}$. Carapace not so smooth, scattered granules and lines of granules quite evident to sight and touch ..... 10
9. Submesial pair of frontal teeth vestigial (Pacific; Baja California and Golfo de California) bellicosus. $9^{\prime}$. Submesial pair of frontal teeth small but definitely formed (Atlantic; United States-Gulf of Mexico) similis.
10. Carapace coarsely granulated; all anterolateral teeth except first two curved forward, without shoulders (Atlantic; Bermuda-Florida-South America-West Africa) .... marginatus.
$10^{\prime}$. Carapace finely granulated; only last or last two anterolateral teeth curved forward, remainder with shoulders ..... 11
11. Submesial pair of frontal teeth absent or vestigial (Atlantic; Bermuda-North America- South America) ornatus.
11'. Submesial pair of frontal teeth never vestigial, but no more than half length of lateral pair ..... 12
12. Lateral spine almost always less than three times length of preceding anterolateral tooth; tips of anterolateral teeth forming a decided arc; males with distal portion of first gonopods almost straight ..... 13
$12^{\prime}$. Lateral spine almost always three or more times length of preceding anterolateral tooth; at least second to fifth anterolateral teeth with tips in a nearly straight line; males with distal portion of first gonopods S-curved (Atlantic; West Africa)
gladiator.
13. First gonopods of mature males with subterminal dorsal setae never more than four in number, often inconspicuous or missing (Atlantic; Caribbean-South America) .....
danae.
$13^{\prime}$. First gonopods of mature males with subterminal dorsal row of setae numbering more than four (Pacific; Southern California-Peru; Galápagos Islands)
arcuatus.

## KEY TO MATURE OR NEARLY MATURE MALE CALLINECTES BASED PRIMARILY ON FIRST GONOPODS

Figures 18-21

1. Tips of gonopods falling well short of suture between thoracic sternite VI and mesially
expanded sternite VII
$1^{\prime}$. Gonopods reaching to, almost to, or beyond suture between thoracic sternite VI and mesially expanded sternite VII ..... 5
2. Gonopods well separated from each other, never touching or crossed ..... 3
$2^{\prime}$. Gonopods overlapping each other, often crossed ..... 4
3. Gonopods slender distally, nearly straight, tips bent slightly mesad (Atlantic; United States-Gulf of Mexico) similis.
$3^{\prime}$. Gonopods fairly stout distally, angled toward midline, then abruptly bent forward in a short slender terminal extension (Atlantic; Bermuda-Florida-South America-West Africa) .marginatus.
4. Tips of gonopods lanceolate, continuing in line with shaft, portion proximal to tip armed with short backward pointing spines quite visible at low magnification (Atlantic; Bermuda-North America-South America) ornatus.
$4^{\prime}$. Tips of gonopods not lanceolate, curved mesad, spines on S-curved shank exceedingly small at low magnification (Atlantic; West Africa) ..... gladiator.
5. Tips of gonopods curved abruptly mesad (Atlantic; Caribbean-South America)$5^{\prime}$. Tips of gonopods not curved abruptly mesad6
6. Slender portion of gonopods almost straight, minutely spined (under magnification), tips almost always bent ventrolaterally, never extending beyond abdominal locking tubercle on thoracic sternite V ..... 7
$6^{\prime}$. Slender portion of gonopods definitely curved or sinuous, variously spined, tips never bent ventrolaterally ..... 8
7. Gonopods with subterminal dorsal setae never more than four in number, often incon- spicuous or missing (Atlantic; Caribbean-South America) ..... danae.
$7^{\prime}$. Gonopods with subterminal dorsal row of setae numbering more than four (Pacific; Southern California-Peru; Galápagos Islands) ..... arcuatus.
8. Tips of gonopods reaching well beyond abdominal locking tubercle on thoracic sternite $V$ ..... 9
$8^{\prime}$. Tips of gonopods not reaching beyond abdowinal locking tubercle on thoracic sternite V (Pacific; Baja California and Golfo de California) bellicosus
9. Slender portion of gonopods with spinules small under magnification and most dense near middle, absent near tip (Pacific; Baja California-Juan Fernández) toxotes.
$9^{\prime}$. Slender portion of gonopods with spinules readily visible at low magnification and distributed to tip ..... 10
10. Gonopodal spines arranged in a broad dorsolateral band ..... 11
$10^{\prime}$. Gonopodal spines arranged in a single, rather uneven dorsolateral row (a few tiny spines lying outside row) (Atlantic; Western Hemisphere, introduced in Europe) ..... sapidus.
11. Tips of all frontal teeth reaching same level ..... 12
$11^{\prime}$. Submesial pair of frontal teeth definitely shorter than lateral pair (Atlantic; West Africa) latimanus.
12. Four frontal teeth with rather rounded tips, lateral pair more broadly triangular and with mesial side having more oblique slope than lateral side
12 . Four frontal teeth acute, lateral pair usually broader than submesial pair (Atlantic; Mexican Gulf coast)
rathbunae.
13. Anterolateral teeth trending forward, their anterior margins shorter than posterior; vestiges of reddish color usually persisting in preserved specimens (except longpreserved ones); (Atlantic; Caribbean-South America) .................................
13 . Anterolateral teeth directed outward their tips acuminate and margins shouldered at
least in anterior portion of row; vestiges of greenish color usually persisting in
13 . Anterolateral teeth directed outward their tips acuminate and margins shouldered at
least in anterior portion of row; vestiges of greenish color usually persisting in preserved specimens (except in long-preserved ones); (Atlantic; Venezuelan estuaries)
bocourti.
maracaiboensis.

## CALLINECTES MARGINATUS (A. MILNE EDWARDS)

Figures 3, 18a, 20a, 22b, 27

Neptunus marginatus A. Milne Edwards, 1861, p. 318, pl. 30, fig. 2 (syntypes: 3 o dry, MNHNP 895-1S, 895-2S, 896, Gabon).
Callinectes larvatus Ordway, 1863, p. 573 [8] (syntypes: 1 万, MCZ 5147, Tortugas, Fla., USA; 3 f, 1 q, MCZ No. 5151, Key West, Fla., USA; 3 ̊ MCZ 5152, Bahamas; 1 ô, 1 juv ㅇ [not ô], MCZ 5155, Jeremie, Haiti).- Smith, 1869, p. 9.- A. Milne Edwards, 1879, p. 225 (var. of C. diacanthus).- Rathbun, 1896, p. 358, pl. 18, pl. 24, fig. 5; pl. 25, fig. 4; pl. 26, fig. 4; pl. 27, fig. 4.- Rankin, 1898, p. 232.- Young, 1900, p. 188 (var. of C. diacanthus).- Doflein, 1904, p. 99.

Neptunus diacanthus.- Brocchi, 1875, pl. 16, fig. 76 [?].- de Man, 1883, p. 150.- Pfeffer, 1890, p. 5, pl. 1, figs. 5, 6.

Callinectes africanus A. Milne Edwards, 1879, p. 229 (var. of C. diacanthus) (syntypes: MNHNP, Cape Verde Islands, not found in 1968).- A. Milne Edwards and Bouvier, 1900, p. 71 (var. of C. diacanthus) (not pl. 4 , fig. $5=$ C. sapidus).
Callinectes larvatus var. africanus? Benedict, 1893, p. 537.
Neptunus (Callinectes) diacanthus.- Ortmann, 1894, p. 77 (part; specimen b, Cuba).
Callinectes marginatus.- Rathbun, 1897, p. 149.1900a, p. 291.- 1900b, p. 142.- 1901, p. $48 .-$ 1921, p. 395, text-fig. 2, pl. 19, fig. 1; pl. 20, fig. 1.- 1930, p. 123, figs. 15e, 16d, 17d, 18c, pl. 53.- 1933, p. 49.- 1936, p. 383.- de Man, 1900, p. 41, pl. 1, fig. 5 (juv \&, not ${ }^{\text {f).- Nobili, }}$ 1906, p. 305.- Gruvel, 1912, p. 3, 6, pl. 2, fig. 1.- Balss, 1921, p. 58.- Odhner, 1923, p. 21.-

Boone, 1927, p. 32.- Contreras, 1930, p. 235, fig. 6.- Vilela, 1949, p. 59.- Capart, 1951, p. 134, fig. 48.- Chace, 1956, p. 154.- Chace and Hobbs, 1969, p. 131, fig. 37d.- Monod, 1956, p. 208, figs. 238, 239.- Rossignol, 1957, p. 82.Guinot and Ribeiro, 1962, p. 48.- Forest and Guinot, 1966, p. 65.- Taissoun, 1973, p. 39, figs. 4A, 5B, photo 7.
Callinectes diacanthus.- Young, 1900, p. 186 (part).
Callinectes marginatus var. larvatus.- Verrill, 1908a, p. 368, text-fig. 22b, pl. 18, fig. 1.

Description.-Carapace (Figure 3) bearing four frontal teeth, submesial pair no more than half length of lateral pair. Central trapezoidal (metagastric) area short, anterior width about 2.4 times length, posterior width about 1.5 times length. Anterolateral margins arched slightly; anterolateral teeth exclusive of outer orbital and lateral spine without shoulders, usually trending forward and anterior margins of all except first two concave, last two teeth spiniform. Lateral spine moderately long and slender. Surface coarsely granulate anterior to prominent epibranchial line and over mesobranchial regions, more finely and closely granulate on proto- and mesogastric areas, prominent branchial lobes, and especially on cardiac lobes; posterior and posterolateral margins smooth.

Chelipeds with smoothly granulate prominent ridges on propodi and reduced ones on carpi; fingers compressed but broadened dorsoventrally producing a pointed spatulate shape; major chela with usual enlarged proximal tooth on dactyl opposing propodal molariform complex, propodus often with decurved lower margin.

Male abdomen and telson narrow, reaching slightly beyond suture between sternites IV and V; telson about 1.8 times longer than wide; sixth
Table 1.-Mean measurements $(\bar{x})$ in mm, with standard deviations (s) and sample sizes ( $N$ ), of selected characters for adult male Callinectes. Refer to Figures 1 and 2 for

| Measurements | arcuatus |  |  |  | bellicosus |  |  | bocourti |  |  |  | danae |  |  | exasperatus |  |  |  | giadiator |  |  |  | latimanus |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | $\bar{x}$ |  | $s$ | $N$ | $\bar{x}$ | $s$ | $N$ | $\bar{x}$ |  | $s$ | $N$ | $\bar{x}$ | $s$ | $N$ | $\bar{\chi}$ |  | $s$ | $N$ | $\overline{7}$ |  | $s$ | $N$ | $\bar{x}$ |  | $s$ | $N$ |
| Length | 42.3 | $\pm$ | 7.4 | 74 | 58.5 | $\pm 17.0$ | 28 | 55.0 | $\pm$ | 9.0 | 46 | 46.5 | $\pm 5.8$ | 84 | 52.6 | $\pm$ | 7.0 | 54 | 35.0 | $\pm$ | 6.3 | 23 | 53.9 | $\pm$ | 10.4 | 27 |
| Width |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| incl. lat. spines | 94.0 |  | 18.7 | 75 | 118.3 | 33.7 | 28 | 109.3 |  | 20.0 | 45 | 108.7 | 14.7 | 84 | 101.6 |  | 14.0 | 54 | 87.0 |  | 15.4 | 23 | 112.8 |  | 23.2 | 26 |
| base lat. spines | 74.5 |  | 13.9 | 75 | 104.5 | 31.0 | 28 | 94.5 |  | 15.7 | 45 | 83.4 | 10.7 | 84 | 89.2 |  | 12.2 | 54 | 65.3 |  | 11.7 | 23 | 96.3 |  | 22.6 | 27 |
| Max. height | 24.6 |  | 4.5 | 74 | 33.4 | 9.5 | 25 | 31.9 |  | 5.2 | 45 | 25.8 | 3.4 | 84 | 31.6 |  | 4.4 | 54 | 20.8 |  | 4.2 | 23 | 32.1 |  | 12.0 | 27 |
| Metagastric |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| ant. width | 17.18 |  | 3.08 | 74 | 24.59 | 7.22 | 25 | 19.73 |  | 3.48 | 46 | 18.91 | 2.48 | 84 | 21.40 |  | 2.96 | 54 | 14.4 |  | 2.70 | 23 | 20.10 |  | 4.28 | 27 |
| length | 7.08 |  | 1.38 | 74 | 8.97 | 2.85 | 25 | 9.95 |  | 1.74 | 46 | 7.71 | 1.12 | 84 | 9.03 |  | 1.39 | 54 | 5.52 |  | 1.10 | 23 | 9.74 |  | 2.12 | 27 |
| post. width | 9.41 |  | 1.72 | 74 | 14.16 | 3.96 | 26 | 10.42 |  | 1.85 | 46 | 10.92 | 1.50 | 84 | 11.25 |  | 1.66 | 54 | 8.34 |  | 1.65 | 23 | 10.35 |  | 2.13 | 27 |
| Telson |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| length | 5.12 |  | 0.89 | 66 | 6.97 | 1.88 | 27 | 9.82 |  | 1.84 | 44 | 5.51 | 0.83 | 82 | 6.63 |  | 1.04 | 52 | 4.39 |  | 0.72 | 23 | 9.72 |  | 1.88 | 26 |
| width | 3.37 |  | 0.51 | 67 | 4.57 | 0.92 | 27 | 4.86 |  | 0.61 | 44 | 3.73 | 0.62 | 81 | 4.40 |  | 0.82 | 52 | 2.73 |  | 0.41 | 23 | 5.13 |  | 0.83 | 26 |


| Measurements | maracaiboensis |  |  | marginatus |  |  |  | ornatus |  |  |  | rathbunae |  |  |  | sapidus |  |  | similis |  |  |  | toxotes |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | $\overline{\bar{x}}$ | $s$ | $N$ | $\overline{\bar{x}}$ |  | $s$ | $N$ | $\bar{\chi}$ |  | $s$ | $N$ | $\overline{\bar{x}}$ |  | $s$ | $N$ | $\bar{x}$ | $s$ | $N$ | $\overline{7}$ |  | $s$ | $N$ | $\bar{\square}$ | $s$ | $N$ |
| Length | 57.8 | $\pm 7.8$ | 11 | 42.6 |  | 6.4 | 82 | 41.6 | $\pm$ | 7.8 | 81 | 52.8 | $\pm$ | 5.2 | 5 | 63.2 | $\pm 13.9$ | 65 | 43.3 | $\pm$ | 5.8 | 26 | 71.3 | $\pm 11.6$ | 24 |
| Width |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| incl. lat. spines | 113.7 | 16.8 | 11 | 93.8 |  | 14.7 | 82 | 91.2 |  | 16.4 | 80 | 112.8 |  | 13.4 | 5 | 142.8 | 35.2 | 65 | 97.6 |  | 13.1 | 26 | 153.1 | 27.5 | 24 |
| base lat. spines | 97.8 | 12.7 | 11 | 77.5 |  | 12.5 | 82 | 72.5 |  | 14.0 | 81 | 92.2 |  | 9.4 | 5 | 115.1 | 26.3 | 65 | 75.7 |  | 10.4 | 26 | 125.9 | 21.9 | 24 |
| Max. height | 33.1 | 4.2 | 11 | 24.6 |  | 3.8 | 81 | 23.6 |  | 4.8 | 81 | 30.4 |  | 3.4 | 5 | 36.4 | 8.5 | 61 | 23.5 |  | 3.2 | 26 | 39.8 | 6.3 | 24 |
| Metagastric |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| ant. width | 21.21 | 2.64 | 8 | 17.05 |  | 2.74 | 82 | 18.75 |  | 3.95 | 81 | 18.92 |  | 2.73 | 5 | 23.60 | 5.32 | 65 | 18.64 |  | 2.94 | 26 | 25.53 | 4.25 | 24 |
| length | 8.81 | 3.66 | 9 | 7.11 |  | 1.22 | 82 | 6.57 |  | 1.30 | 81 | 9.30 |  | 1.09 | 5 | 10.60 | 2.59 | 65 | 6.81 |  | 1.04 | 26 | 12.14 | 2.07 | 24 |
| post. width | 8.15 | 4.04 | 8 | 10.60 |  | 1.49 | 82 | 11.49 |  | 2.07 | 81 | 9.80 |  | 1.54 | 5 | 12.85 | 2.89 | 65 | 11.09 |  | 1.55 | 26 | 12.11 | 2.12 | 24 |
| Telson |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| length | 14.08 | 1.23 | 11 | 5.74 |  | 1.18 | 79 | 4.99 |  | 1.02 | 78 | 9.56 |  | 0.95 | 5 | 9.95 | 2.42 | 65 | 5.25 |  | 0.75 | 26 | 10.91 | 1.71 | 23 |
| width | 6.07 | 0.44 | 11 | 3.19 |  | 0.59 | 79 | 3.04 |  | 0.54 | 78 | 4.74 |  | 0.44 | 5 | 5.66 | 1.23 | 65 | 3.65 |  | 0.37 | 26 | 5.93 | 0.68 | 23 |

Table 2.-Mean measurements $(\overline{\boldsymbol{x}}$ ) in mm, with standard deviations (s) and sample sizes ( $\mathbf{V}$ ), of selected charaters for adult female Callinectes. Refer to Figures 1 and 2 for

| Measurements | arcuatus |  |  | bellicosus |  |  | bocourti |  |  | danae |  |  | exasperatus |  |  | gladiator |  |  | latimanus |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | $\bar{x}$ | $s$ | $N$ | $\overline{\bar{x}}$ | $s$ | $N$ | $\bar{x}$ | $s$ | $N$ | $\bar{x}$ | $s$ | $N$ | $\bar{\chi}$ | $s$ | $N$ | $\bar{x}$ | $s$ | $N$ | $\bar{x}$ | $s$ | $N$ |
| Length | 36.5 | $\pm 8.1$ | 30 | 56.4 | $\pm 6.6$ | 16 | 51.6 | 6.7 | 30 | 40.8 | $\pm 3.9$ | 52 | 49.5 | $\pm 5.0$ | 32 | 29.9 | 5.7 | 45 | 53.5 | $\pm 4.9$ | 19 |
| Width |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| base lat. spines | 62.9 | 14.0 | 30 | 97.0 | 12.1 | 16 | 88.1 | 11.3 | 31 | 71.7 | 7.1 | 51 | 82.8 | 8.6 | 32 | 54.8 | 10.1 | 45 | 94.5 | 9.0 | 19 |
| Max. height | 22.0 | 5.2 | 29 | 33.6 | 4.4 | 16 | 31.0 | 4.2 | 30 | 23.7 | 2.3 | 52 | 30.8 | 3.4 | 31 | 18.7 | 3.5 | 45 | 32.3 | 3.1 | 18 |
| Metagastric |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| ant. width | 16.02 | 3.34 | 29 | 24.70 | 2.85 | 15 | 19.76 | 2.90 | 30 | 17.57 | 1.78 | 52 | 21.90 | 2.18 | 32 | 13.03 | 2.11 | 44 | 20.94 | 3.99 | 19 |
| length | 6.34 | 1.46 | 29 | 9.43 | 0.96 | 15 | 9.72 | 1.27 | 30 | 7.00 | 0.81 | 52 | 8.85 | 1.01 | 32 | 4.93 | 1.10 | 44 | 10.05 | 1.06 | 19 |
| post. width | 9.14 | 1.98 | 29 | 14.38 | 1.30 | 15 | 10.90 | 1.75 | 30 | 10.47 | 1.13 | 52 | 11.85 | 1.30 | 32 | 7.65 | 1.21 | 44 | 11.67 | 1.10 | 19 |
| Telson |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| length | 4.19 | 1.01 | 30 | 6.92 | 0.97 | 16 | 7.76 | 1.19 | 29 | 4.94 | 0.56 | 50 | 6.25 | 0.79 | 31 | 3.65 | 0.94 | 45 | 8.03 | 0.97 | 19 |
| width | 4.39 | 0.95 | 30 | 7.02 | 0.75 | 16 | 6.53 | 0.83 | 29 | 5.04 | 0.50 | 50 | 6.54 | 0.80 | 31 | 3.77 | 0.92 | 45 | 7.12 | 0.63 | 19 |
| Abd. seg. length |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 5th | 7.04 | 1.75 | 30 | 11.84 | 1.69 | 16 | 10.70 | 1.56 | 30 | 8.03 | 1.37 | 51 | 10.63 | 1.28 | 32 | 6.14 | 1.59 | 45 | 11.09 | 1.18 | 19 |
| 6th | 7.38 | 1.86 | 29 | 11.76 | 1.49 | 16 | 11.23 | 2.15 | 29 | 8.16 | 0.96 | 48 | 9.89 | 1.10 | 30 | 5.68 | 1.42 | 45 | 13.89 | 7.36 | 19 |


| Measurements | maracaiboensis |  | marginatus |  |  | ornatus |  |  | rathbunae |  |  | sapidus |  |  | similis |  |  | toxotes |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | $\overline{\bar{x}}$ | $N$ | $\bar{x}$ | $s$ | $N$ | $x$ | $s$ | $N$ | $\overline{\bar{x}}$ | $s$ | $N$ | $\bar{x}$ | $s$ | $N$ | $x$ | $s$ | $N$ | $\bar{x}$ | $s$ | $N$ |
| Width |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| incl. lat. spines | 114.3 | 3 | 83.5 | 8.5 | 42 | 77.7 | 12.5 | 43 | 126.6 | 12.6 | 5 | 131.0 | 34.3 | 69 | 76.9 | 11.8 | 39 | 148.9 | 11.5 | 13 |
| base lat. spines | 91.7 | 3 | 68.9 | 6.9 | 42 | 29.5 | 4.8 | 43 | 101.6 | 12.0 | 5 | 99.4 | 24.1 | 68 | 60.9 | 9.0 | 39 | 117.9 | 7.6 |  |
| Max. height | 31.3 | 3 | 23.3 | 2.5 | 42 | 20.5 | 4.3 | 42 | 34.0 | 5.0 | 5 | 31.8 | 7.9 | 64 | 19.8 | 2.9 | 39 | 39.4 | 2.6 | 13 |
| Metagastric |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| ant. width | 20.40 | 3 | 16.23 | 2.46 | 41 | 16.86 | 2.96 | 42 | 22.88 | 3.36 | 5 | 21.66 | 4.97 | 69 | 15.77 | 3.09 | 39 | 25.80 |  | 13 |
| length | 9.53 | 3 | 6.69 | 0.80 | 41 | 5.88 | 1.04 | 42 | 10.12 | 1.34 | 5 | 9.38 | 2.39 | 69 | 5.70 | 0.89 | 39 | 12.00 | 0.69 |  |
| post. width | 11.23 | 3 | 10.24 | 1.33 | 41 | 10.46 | 1.97 | 42 | 12.64 | 2.46 | 5 | 12.13 | 2.67 | 69 | 9.67 | 1.41 | 39 | 13.10 | 1.03 | 13 |
| Teison |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| length | 8.20 | 3 | 5.11 | 0.56 | 40 | 4.24 | 0.86 | 43 | 8.24 | 1.51 | 5 | 7.94 | 1.91 | 67 | 4.08 | 0.70 | 39 | 9.48 | 0.64 | 13 |
| width | 7.10 | 3 | 4.91 | 0.53 | 40 | 4.27 | 0.81 | 43 | 7.36 | 1.06 |  | 7.03 | 1.52 | 67 | 4.48 | 0.55 | 39 | 8.16 | 0.76 |  |
| Abd. seg. length 11.27 lin |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| 5th | 11.27 | 3 | 7.93 | 0.93 | 41 | 6.70 | 1.46 | 43 | 12.52 | - 1.86 | 5 | 12.09 | 2.99 | 66 | 7.10 | 1.11 | 39 | 13.88 | 1.32 | 13 |
| 6th | 11.57 | 3 | 8.06 | 0.90 | 39 | 7.04 | 2.93 | 41 | 16.86 | 8.79 | 5 | 11.96 | 3.14 | 65 | 7.30 | 1.18 | 38 | 14.24 | 3.01 |  |

segment nearly parallel sided but somewhat broadened proximally. Mature female abdomen and telson reaching same level as in male, length slightly exceeding width ( 1.05 times); sixth segment longer than fifth. First gonopods of male (Figures 18a, 20a) short, reaching about midlength of sternite VII, approximating each other or occasionally overlapping at level of sharp distal curve, distal portion abruptly curved laterad, tapered to a rather sharp point, twisted one-fourth turn on axis and, except for membranous spoutlike tip, armed with minute scattered retrogressive spinules tending to arrangement in rows, a few spinules proximal to flexure. Gonopores of female (Figure 22b) ovate with apex on long axis directed anteromesad, aperture of each with margin irregularly rounded and sinuous except on mesial side where it slopes from surface laterad under superior anterior border.

Size of carapace in mm.-Largest male: length 67 , width at base of lateral spines 118 , including lateral spines 142. Largest female: length 49 , width at base of lateral spines 82 , including lateral spines 95 . Mature size of females varies considerably, the smallest examined having a carapace length of 33 and width including lateral spines of 70 . Summary of selected measurements is given in Tables 1 and 2.

Color.-Carapace brown with areas of bluish black. Chelae brown above; fingers dark on external face except for tips and proximal portion, internal face dark in distal two-thirds; dark color of fingers retained in preservation (in part from Rathbun, 1930, and pers. commun. from Charles A. Johnson). Milne Edwards and Bouvier (1900) gave essentially the same impression, characterizing the entire carapace, abdomen, external face of chelipeds, posterior legs, some areas of the walking legs with their marginal hairs as greenish brown and other parts of the appendages as a beautiful blue, but there is some confusion here because the colored plate accompanying this description (Plate 4, Figure 5) represents C. sapidus. Rossignol (1957) described the carapace as marbled, and recently preserved material in alcohol sometimes does give an impression of mottled gray and white on the carapace.

Variation.-The carapace in C. marginatus shows a number of individual variations. The small anterolateral teeth generally trend forward,
but there is enough individual departure from this pattern to cause confusion. Teeth in the mesial part of the row trend forward more than those in the lateral part, the first three often being rounded while the last four are pointed. Small anterolateral teeth on syntype females in MNHNP do not definitely trend forward, and those on the syntype of C. larvatus (MCZ 5155) are well separated, with apices directed outward rather than hooked forward. There are differences, too, in width of the anterolateral teeth, a suggestion of narrower teeth in Brazil than in Florida, and broad teeth on some African material. Occasionally there is some iridescence along the anterolateral border, and often hairiness along the lower anterolateral border.

The inner orbital fissures are usually tightly closed, sometimes with a slight notch on the orbital border, but open in some African and Dutch West Indies (Aruba) material.

The anterolateral slopes have an arching concavity proximal to the bases of the anterolateral teeth and extending transversely behind the orbitofrontal region that is more pronounced than in other species of the genus. This is especially evident in mature females. The abdomen of immature males is flush with the sternum and relatively wider than in adults in which it is somewhat recessed. Among mature males, calcification is weak in the articulation between the fifth and sixth abdominal segments allowing definite flexure in this joint, but transverse ridges ("stops") on external exposed edges of the joint prevent doubling backward. The calcification pattern is well demonstrated in two mature males in USNM 4172 from Dominican Republic. Abdominal segment 6 is constricted at mid-length in some males. The abdomen of adult females resembles that of C. ornatus.

Sexual differences include a more tumid appearing body among females than males, an effect resulting partly from less produced lateral spines, as well as granulations on the carapace that are relatively more prominent than on males. Granules on the carapace sometimes are very coarse in front of the epibranchial line, but seldom as coarse behind as in front of this line. Inconspicuous spination on the male first gonopods in specimens from the Canal Zone of Panama, Honduras, Colombia, and Venezuela is not so strong nor dense as that in males from Florida where there is a suggestion that the scattered spines are in rows proximal to the distal bend; spination
seems entirely lacking in some Brazilian material.
This is the species that should be named "latimanus" because broad, spatulate, often strongly asymmetrical chelae occur on both juveniles and adults. The chelipeds often seem heavy for the size of the animal bearing them, but pronounced asymmetry is not universally present. Some individuals have both chelae basically alike except for size, and in almost all except juveniles the ventral side of the propodus (especially the major) is decurved in a wide sweep giving emphasis to the "spatulate" character. The proximal tooth on the dactyl of the major chela may be moderate but is often large in size and worn as shown in Figure 3a. Some juveniles with worn chelae have a gape between fingers of the minor as well as major chela along with development of a strong proximal tooth on the dactyls. Although similarity in chelae may indicate regeneration, there is no evidence that replacement has occurred.

Habitat.-Meager data recorded with specimens suggests that this species lives in a variety of shallow littoral environments probably seldom exceeding 15 m (rarely to 25 m [?]) and usually in much shallower water from intertidal pools to 3 $m$ deep. Most specimens have been collected by hand, seine, dip net, etc., from sand and mud flats, algae and grass flats, sandy beaches, rocky pools, eroded coral bases, oyster bars, shallows at edge of mangroves, and at the surface under lights at night. A number of authors (Milne Edwards and Bouvier, 1900; Monod, 1956; Rossignol, 1957; Forest and Guinot, 1966; Coêlho, 1967a, b, 1970) have noted that C. marginatus is a coastal species limited to depths of a few meters, often in brackish water, but rather rare and never as abundant as other species of Callinectes. Capart (1951) found it on shallow mud bottoms in salinities varying from $7.43-14.85 \%$ at the surface to $19.29-32.56 \%$ in $5-\mathrm{m}$ depths and in a bottom temperature range of $22.5^{\circ}$ to $27.42^{\circ} \mathrm{C}$; he never found it in the ocean. Buchanan (1958) similarly found it in $5.5-14-\mathrm{m}$ depths in a temperature range of $27^{\circ}$ to $30^{\circ} \mathrm{C}$ off Accra, Ghana, in what he termed the inshore fine sand community. Chace (1956) recorded it in $27.5^{\circ} \mathrm{C}$ water off Los Roques, Venezuela.

Spawning.-Both the museum material studied and records in literature yield only fragmentary evidence on spawning. Ovigerous females are re-
corded from December to July in various parts of the geographic range on both sides of the Atlantic. Specifically the records are: Congo and St. Thomas, December; St. Thomas, January; Grenadines and Cuba, March; Haiti, April; Jamaica and Senegal, May; Colombia, Curaçao and São Tomé (Forest and Guinot, 1966), June; Florida and Puerto Rico, July.

Distribution.-Off southern Florida through Caribbean Sea to south central Brazil off Estado de São Paulo; Bermuda and Cape Verde Islands; Senegal to central Angola (Figure 27). A recent record from North Carolina is regarded as a temporary range extension.

Economic importance.—Gravel (1912), describing fisheries for C. latimanus along the Gulf of Guinea, noted that C. marginatus is also caught all along the coast from Senegal to the Congo under a variety of local names.

Remarks.-The populations on each side of the Atlantic seem indistinguishable by means of external morphological characters. Different names applied to the populations on each side reflect the discontinuity of early collections, Verrill (1908a) for instance considering larvatus the American and africanus the African variety, but with the progress of exploration and inventory it is evident that the whole is a genetic continuum with minor local variations already pointed out. Most modern workers (Capart, 1951; Monod, 1956) accept this idea although deploring the difficulty in identifying juveniles.

Verrill (1908b) early recognized the significance of larval transport in oceanic currents, applying it to populations of C. marginatus in Bermuda that have their origin in the West Indies. It is tempting to make the generalization that this species in its moderate size, short, simply ornamented male first gonopods, and amphi-Atlantic pattern of geographic distribution possibly represents an unspecialized and primitive member of the genus, but such ideas are qualified by the specialization of chelae seemingly well adapted by their dorsoventrally broadened but rather thin fingers for reaching into crevices, perhaps into mollusk shells after they are cracked. In short, generalized structure is hard to assess.

Some specimens show evidence of massive fouling by the barnacle Chelonibia. A male (dry) from Brazil (BMNH 48.86) measuring 89 mm between
tips of lateral spines bears the basal disc of a bar－ nacle measuring $24.9 \times 26.2 \mathrm{~mm}$ ，or an oval area covering all of the metagastric and a portion of the right branchial lobe forward to the base of the frontal margin and edge of the right orbit．A sec－ ond and still intact barnacle covers all of the left mesobranchial region（ $11.7 \times 13.0 \mathrm{~mm}$ ）．

Material．－Total． 242 lots， 615 specimens．
Specimens listed in Rathbun（1930）from USNM（31091，4172，24445，24446，24447，24448， 24449，24450，24454，43905，62684，54255 not found； $32514=$ C．ornatus， $33103=$ C．similis， 61364 ＝C．danae）and MCZ．

USNM． 99 lots， 282 specimens，including the following not cited above：

## UNITED STATES

Florida：80624，Lake Worth，1945， 1 o，A．H． Verrill．113458，Pigeon Key，Monroe Co．， 7 Aug． 1965， 1 or，R．B．Manning．123063，Bahia Honda Key，Monroe Co．， 14 June 1964， 2 б， 2 juv，Foster and Kaill，No．64－11－I．71635，Key West，1934， 1 \％，H．H．Darby．76972，Key West，no date， 5 f， 1 i （ov），C．J．Maynard．123075，Key West，no date， 3 of， 2 \＆，U．S．Bur．Fish．The following from Dry Tortugas－62156， 25 July 1928，（juv） 2 \＆，A．S． Pearse．76968，Fort Jefferson，Aug．1930， 1 九，W． L．Schmitt．62155，Loggerhead Key， 6 Aug．1928， 2 ô（juv），A．S．Pearse． 76967 and 76970，Long Key， 25 June 1931， 1 ठ， 5 juv，W．L．Schmitt．76969， Long Key－Bush Key， 18 June 1932， 1 d，W．L． Schmitt．71636，Bush Key， 4 Aug．1934， 1 \＆，H．H． Darby．71655，Sarasota Bay，summer 1930， 1 juv， W．W．Wallis．

## BAHAMAS

101130，Bimini Bay， 27 Nov．1951， 1 o（juv），F． Frieders．

## CUBA

99977，E Xanadú，Hicacos Pen．，Matanzas Prov．，24－27 Jan．1957， 1 carapace，W．L．Schmitt．

## JAMAICA

123060，N shore， $18^{\circ} 24.5^{\prime} \mathrm{N}, 77^{\circ} 07^{\prime} \mathrm{W}, 20$ May 1965， 1 ¢（ov），Oregon Stn．5405．123062，Kingston Harbor， 17 May 1965，I \＆，B．B．Collette．

## HAITI

65859，Ile a Vache， 29 Apr．1930， 1 ¢（ov），W．M． Parish．81481，I．opposite Bayeaux， 23 June 1941， 1 九，H．H．Bartlett．

DOMINICAN REPUBLIC
62828，near Montecristi，winter 1928－29， 1 chela，H．W．Kreiger．

## PUERTO RICO

73282，off Fort San Gerónimo，San Juan， 30 Apr．1937， 3 万，W．L．Schmitt．73285，near Fort San Gerónimo，W end San Juan I．， 27 Mar．1937， 1 q， W．L．Schmitt．

## VIRGIN ISLANDS

St．Croix： 72351 and 72359，Salt River Bay， 1935－36， 2 đt，H．A．Beatty．73284，Christiansted， 9 Apr．1937， 1 o，W．L．Schmitt． 76964 and 76965， Envy Bay，no date， 1 of， 2 ㅇ，H．A．Beatty．Prickly Pear I．123070，Vixen Pt．，Gorda Sound， 15 Apr． 1956， 1 ㅇ（juv），Nicholson，Schmitt，and Chace．

## BARBUDA

123069，near Oyster Pond Landing， 6 Apr．1956， 1 今，Schmitt，Chace，Nicholson，and Jackson．

## ANTIGUA

123068，Tank Bay，English Harbor， 3 Apr．1956， 3 o，Schmitt，Chace，Nicholson，and Jackson．

## GUADELOUPE

123067，between Monroux and Rat Is．，Pointe à Pitre，30－31 Mar．1956， 21 §， 5 \＆， 13 juv，Chace and Nicholson．

## ST．LUCIA

123066，shore of bay outside Marigot Lagoon， 21 Mar．1956， 1 f，Chace，Nicholson，and crew．

## GRENADINES

123064，Tyrrell Bay，Carriacou I．， 15 Mar．1956， 3 ¢（ov），Schmitt and Nicholson．123065，Tyrrell Bay，Carriacou I．， 16 Mar．1956， 1 \＆，D．V．Nichol－ son．

## MEXICO

Quintana Roo：123072，Cozumel I．，near light－ house at Punta Molas， 9 Apr．1960， 5 §＇，Rehder and Bousfield．123071，Bahía del Espíritu Santo，north shore near Lawrence Pt．， 6 Apr．1960， 1 \＆，Rehder， Daiber，and Haynes．123073，Pt．Santa María ［ $20^{\circ} 19^{\prime}$ N， $86^{\circ} 59^{\prime}$ W］， 22 Apr．1960， 1 o，Schmitt and Rehder．

## HONDURAS

78107，Utila I．，Sept．1938， 1 §，L．Mouquin．

