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THE SWIMMING CRABS OF THE GENUS *CALLINECTES* (DECAPODA: PORTUNIDAE)

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ABSTRACT

The genus *Callinectes* and its 14 species are reevaluated. Keys to identification, descriptions of species, ranges of variation for selected characters, larval distribution, and the fossil record as well as problems in identification are discussed. Confined almost exclusively to shallow coastal waters, the genus has apparently radiated both northward and southward from a center in the Atlantic Neotropical coastal region as well as into the eastern tropical Pacific through continuous connections prior to elevation of the Panamanian isthmus in the Pliocene epoch and along tropical West Africa. Eleven species occur in the Atlantic, three in the Pacific. *Callinectes marginatus* spans the eastern and western tropical Atlantic. *Callinectes sapidus*, with the broadest latitudinal distribution among all the species (Nova Scotia to Argentina), has also been introduced in Europe. All species show close similarity and great individual variation. Both migration and genetic continuity appear to be assisted by transport of larvae in currents. Distributional patterns parallel those of many organisms, especially members of the decapod crustacean genus *Penaeus* which occupy similar habitats.

The blue crab, *Callinectes sapidus* Rathbun, a staple commodity in fisheries of eastern and southern United States, is almost a commonplace object of fisheries and marine biological research, but its taxonomic status has been questionable for a long time. Other members of the genus also have questionable taxonomic status, and they are difficult to identify. In a time when expanding interest in species easily exploitable for food has generated new research, we can benefit from a fresh look at the component species of this important genus in order that major areas of study such as fisheries biology, ecology, zoogeography, embryology, and physiology can proceed on a stable nomenclatural basis. The purposes of this paper are to: 1) synonymize nomenclature, 2) characterize the species, 3) discuss variation in morphology, 4) provide illustrations and keys to identification, 5) delineate geographic distribution of species, 6) provide remarks on ecological associations, 7) contribute to resolution of the fossil record, and 8) document evidence and provide a list of identified specimens in major museums of the world.

HISTORY

Crabs of the genus *Callinectes* have an anecdotal record dating from early explorations of the Western Hemisphere. Perhaps the earliest listing among natural assets in the New World is Thomas Hariot's (1588) mention of "*Sea crabbes,* such as we have in England." A similar record is Marcgrave's account in 1648 (Lemos de Castro, 1962) of a South American *Callinectes* [= *danae* Smith (1869)], one of the common portunids used for food. D. P. de Vries in 1655 (Holthuis, 1958) referred to the eating qualities of blue crabs in the New York area and likened the white and orange color of their chelipeds [females] to colors of the House of Orange. Lawson (1714), recounting his years among the Indians in the Carolinas, may have initiated the tale of raccoons fishing for crabs in marshes with their tails, but more factually he wrote [undoubtedly of the blue crab, *C. sapidus* Rathbun (1896)], "the smaller flat Crabs I look upon to be the sweetest of all Species . . . the Breadth of a lusty Man's Hand . . . . These are inumerable, all over the salts of Carolina . . . taken not only to eat, but are the best Bait for all sorts of Fish, that live in the Salt-Water."

Holthuis (1959) thought that de Geer (1778) probably represented *Callinectes bocourti* A. Milne Edwards (1879) under the name "Crab de l'ocean" when he described a swimming crab from Surinam in general terms as *Cancer pelagicus*. Ordway (1863) considered de Geer's species synonymous with *Lupa sayi* Gibbes (1850), and Rathbun (1896:350) stated "Figures 8, 9 and 11 correctly represent neither of these species, nor are they applicable to any species of *Callinectes,* while, on the other hand, Figure 10 shows the narrow abdomen characteristic of that genus." Since *C. bocourti* is the commonest portunid in Surinam, abundant enough to be marketed, and

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certain of de Geer's figures can be interpreted as *Callinectes*, Holthuis's conclusion seems reasonable.

Bosc (1802) gave a thumbnail natural history sketch for *C. sapidus* in South Carolina comparing crudely in its accuracy with some modern accounts, but he used the name *Portunus hastatus* along with a description taken from J. C. Fabricius which applied to a European species.

Thomas Say (1817) was the first naturalist to give a description of the common blue crab of the eastern United States, calling it *Lupa hastata*, in what he intended as a redescription of *Lupa hastata* (Linn.), a species known from the Mediterranean (Rathbun, 1896).

A few years later Latreille (1825) gave the name *Portunus diacantha* to the common blue crab of eastern United States accompanied by a poor description that applied to more than one species. Say and Latreille, plus perhaps De Kay (1844) who published a description and beautifully colored plate of what he called *Lupa dicantha* [= *C. sapidus*] from New York, account for the main early treatments of *Callinectes* by naturalists.

Search of newspaper and popular journal files could yield a harvest of fact and fiction about these crabs culminating perhaps in accounts of the "crab derbies" held in recent years to promote marketing in crab producing states of the eastern seaboard of the United States. Crab stories abound and crab fishing techniques are similar in all countries where *Callinectes* occurs. It is not surprising, therefore, that this profusion has carried over into the scientific literature where scholars have bequeathed a complex nomenclature in numerous contributions.

Scholarly systematic work on the whole genus was last presented by Rathbun in 1896 as a general revision and amended in 1897. There is no need to clutter the text here by recalling the parade of specific epithets employed in the game of taxonomic musical chairs played by a succession of authors. Each built on the foundation of previous work, usually as collections substantially increased in museums, but many minor papers were reports on expeditions extending the bounds of known geographic ranges for certain species. Details of these histories may be followed in the synonymies, but the principal studies should be placed in perspective as an introduction, and in reviewing them I repeat part of Rathbun's (1896) review.

William Stimpson (1860) created the genus *Callinectes* to contain portunids in which the males have a T-shaped abdomen and the merus of the outer maxillipeds is short, sharply prominent, and curved outward at its antero-external angle. He regarded as one species "the common American *Lupa diacantha* (Latreille)" in his new genus, and doubtfully distinguished a second, *L.* (= *Callinectes*) *bellicosa*, which he had described (1859) from the Gulf of California. We now know that the second of Stimpson's generic characters is nearly valueless because other portunids have similar third maxillipeds, but the narrow sixth segment of the T-shaped abdomen of males holds and is reinforced by absence of an internal spine on the carpus of the chelipeds in *Callinectes*.

The limited view of the genus held by Stimpson was soon broadened by Ordway (1863) who recognized nine species distinguished in part by structure of the male first pleopods. Ordway restricted the name *diacanthus* to a Brazilian form described by Dana (1852) which we now know as *C. danae*. The common blue crab of the eastern United States was given Say's (1817) name *hastatus*, Stimpson's *bellicosus* retained, and six new species named. Ordway's study of crustaceans was diverted by the Civil War, and he remained in military life until his death in 1897. Poor communication may have led to Ordway's confusion in nomenclature, but his concept of species based on material then available was remarkably clear.

Latreille's (1825) *diacantha*, though valid, was never widely recognized because of its poor definition. Various "*diacanthas*" were employed for 139 yr finally ending in official suppression of Latreille's ill-starred name in 1964 for purposes of nomenclatural stability. Smith (1869) substituted *C. danae* for Dana's Brazilian *C. diacantha*.

Then followed an interval dominated by A. Milne Edwards's revision of the Portunidae (1861) and his review of the Crustacea of Mexico (1879). Milne Edwards at first did not recognize *Callinectes* as a distinct genus but later accepted it. He conservatively viewed *Callinectes* species as "varieties" of *diacanthus* (adding five new ones to Ordway's nine in 1879), and the influence of his ideas pervaded the field for a long time, leading eventually to Rathbun's revisionary papers. Milne Edwards's reasoning was not without merit for the genus is close to other portunids. Indeed, its validity as a distinct unit was again challenged for a time by Stephenson and Campbell (1959) and Stephenson (1962) during reassessment of

Indo-Pacific Portunidae, but later left intact (Stephenson, Williams, and Lance, 1968).

In 1896 Rathbun recognized the following numbers of species: western Atlantic, six species and one subspecies (Rathbun never treated the nominal subspecies as anything but a full species); eastern Pacific, four species; eastern Atlantic off Africa, one species and one subspecies. The list was almost immediately altered (1897) by name recombinations, elevation of subspecies, description of a new species, and extension of known geographic ranges. This brought the numbers to: western Atlantic, six species and one subspecies; eastern Pacific, four species; eastern Atlantic off Africa, four species. There the inventory rested until 1921 when Rathbun revised the African species, reducing them to three but noting a doubtful subspecies reported from Europe (Bouvier, 1901) greatly resembling *C. sapidus* of the United States. In 1930 Rathbun published the third of a four-volume work that serves as the standard reference on American crabs. In this she reduced the recognized species in the eastern Pacific by one. Collaterally she treated fossil members of the genus, describing three new species from the Oligocene and Miocene of Middle America (1919b), and two more species from similar ages in North America (1935). One of these from the Miocene (=?) of Virginia and Florida was considered identical with living *C. sapidus*.

By 1930 the genus seemed stabilized, but Rathbun herself had introduced confusion in 1907 by describing a juvenile *Portunus* from the South Pacific as *Callinectes alexandri*. This error bore fruit years later in helping to generate doubt concerning validity of the genus (Stephenson and Campbell, 1959). During the same year that Rathbun's cancroid treatise appeared, Contreras (1930) described two new species in a little known paper, one from the Gulf of California and another from the Gulf of Mexico. Capart (1951) and Monod (1956) both supported Rathbun's analysis of West African forms, and in shedding more light on the introduction of *C. sapidus* into European waters (first noticed in 1901) erased Rathbun's doubts about a poorly documented subspecies from that area. They also pointed out difficulties in identifying some specimens. The introduction of *C. sapidus*, documented by numerous authors, was reviewed by Holthuis (1961, 1969). Following petition of Holthuis (1962), the International Commission (1964), to avoid confusion in nomenclature of such a well-known species, made *Callinectes sapidus* Rathbun the type species of the genus and suppressed the long dormant *Portunus diacantha* Latreille, 1825. Garth and Stephenson (1966) confirmed Rathbun's interpretation of the eastern Pacific *Callinectes*, and Williams (1966) described a new species from the Carolinian Province of North America.

Such was the status of the species problem when the present study was undertaken. Numerous authors had expressed difficulty in making identifications, especially of juvenile material. Geographic limits for species seemed ill defined. Few attempts to analyze large series systematically had been attempted, but results of work in fisheries management indicated that populations within species might be distinct. Mindful of this and aware of series of specimens in museums, a review of the group seemed profitable. Simultaneously, Taissoun (1969, 1972) began study of *Callinectes* in Venezuela finding a form endemic to Lake Maracaibo. It is likely that new approaches such as ecological and larval studies may continue to elucidate variation in the genus.

CHARACTERS OF SYSTEMATIC VALUE

The gross features of morphology having greatest usefulness in distinguishing species of *Callinectes* are (Figures 1, 2): viewing dorsally, 1) the number, shape, and arrangement of frontal teeth, 2) shape of the metagastric area, 3) shape and curvature of the anterolateral teeth and the lateral spine, 4) granulation of the dorsal surface; viewing ventrally, shape of male and mature female abdomen. Shape of the chelipeds is also useful, as are the colors in fresh specimens. In addition to gross features, male first pleopods (Figures 18-21) are diagnostic, and shapes of female gonopores (Figures 22-23) are aids to identification.

Body proportions.—Proportions of the body in both sexes change with growth until a characteristically male or female form develops. The carapace of males becomes relatively broader than that of females, with lateral spines accentuated; in especially large individuals of some species the metagastric region tends to be somewhat sunken at its side and rear margins. Females have a dorsally tumid appearance, with the carapace more uniformly inflated and granulated and relatively not so broad nor with lateral spines so accentuated as in males. Body heights are alike in the two sexes.

Spines.—All spiniform characters, poorly developed and rounded at the apices in juveniles, gradually assume conformation characteristic of the species as growth progresses.

Chelipeds.—All species in the genus have the hands of the chelipeds (Figures 3-17) modified into a major chela (crusher, usually on right side) and a minor chela (cutter, usually on left side)—heterochelic and heterodont (Schäfer, 1954; Števčić, 1971). Loss of the major chela induces a well-known reversal at the next molt with the new hand becoming a minor chela. A few individuals have two minors, but almost none exhibit two major chelae. Size and strength of the major hand vary a good deal, each species having a sometimes ill defined but characteristic shape. In all, especially among males, the dactyl of the major chela has a strongly developed proximal tooth which closes against a molariform complex on the propodus (Schäfer, 1954). A decurved lower margin near the base of the propodal finger opposite the proximal crushing apparatus on opposed edges of the fingers accompanies development of the complex, and in huge males of some species is a prominent feature. Teeth distal to the molariform complex of the major chela are more sectorial in structure, but not so sharp as those on the minor hand. Sectorial teeth of both hands tend to be arranged in triads, a large central tooth flanked by smaller ones, but there is much variation. In old individuals no longer molting or molting infrequently, the proximal crusher teeth become worn, occasionally almost obliterated. Size and wear vary with species and are undoubtedly associated with feeding habits. *Callinectes sapidus,* for example, is known to feed on the American oyster, *Crassostrea virginica,* and other mollusks. Other species of *Callinectes* probably have similar feeding habits, but these are not well documented.

Secondary sexual structures.—Immature females have a triangular abdomen (Figure 2) with most segments indistinguishably fused, but at the terminal maturation molt (Churchill, 1919) all segments become free. The abdomen of mature females has a variable but roughly characteristic shape in each species. Distal portions of the abdomen in immature males also have a developing shape which becomes characteristic of the species in adults.

Primary sexual structures.—The copulatory apparatus of male *Callinectes* has been recognized as a good separator of species since the time of Ordway (1863), but until recently no one used fine structure of these organs as serious aid to identification. Snodgrass (1936) and Cronin (1947) both described the external male sexual apparatus, and I here adopt Snodgrass's term "first gonopod" for the first male pleopod. The first gonopod is essentially a narrow flat plate rolled longitudinally into a cylinder that may be variously curved and twisted, terminating in a tip varying from nearly tubular to a simply flared trough. First gonopods of each species have characteristic shapes, but there is individual variation reinforced by age, molt stage, wear, and irregularity in preservation. The distal portion of each first gonopod is armed with retrogressive articulated spinules, exceedingly tiny and rather unevenly distributed in one set of species having short first gonopods—*C. gladiator* Benedict (1893), *marginatus* A. Milne Edwards (1861), *ornatus* Ordway (1863), and *similis* Williams (1966) (Figures 18a-d, 20a-d), as well as in a second set with relatively longer first gonopods—*C. arcuatus* Ordway (1863), *danae,* and *exasperatus* (Gerstaecker, 1856) (Figures 18e-g, 20 e-i), but larger and arranged in longitudinal bands among species with long curved first gonopods in a third set—*C. bellicosus, bocourti, latimanus* Rathbun (1897), *maracaiboensis* Taissoun (1972), *rathbunae* Contreras (1930), *sapidus,* and *toxotes* Ordway (1863) (Figures 18h-j, 19, 20j-p, 21). In the last group, the spinules are irregular in size showing evidence of breakage and replacement during growth. Moreover, first gonopods of certain species bear slender setae. In *C. arcuatus* and *danae,* with first gonopods of moderate length, the setae are subterminal (Figure 20e-h) but in others with longer first gonopods [*C. bellicosus, latimanus, maracaiboensis, rathbunae, sapidus,* and *toxotes* (Figures 20j-p, 21)] they are arranged along the shaft at levels between the fifth to seventh thoracic sternites in a single sternomesial row following the twist of the appendage. The setae are relatively largest in *bellicosus* (Figure 20j, k).

Structure of the female gonopores covered by the abdomen and located near the midline on the sixth thoracic somite (Snodgrass, 1936) is less useful as a specific character than that of the male first gonopod, but even here there are some conformational types. Each gonopore leads via a spermathecal duct (vagina) to a spermatheca which in turn is connected to oviduct and ovary, but it is the gonopore alone that shows crude structural specificity. Hartnoll (1968) showed that the gonopore of portunids is an uncovered structure often rounded laterally and pointed mesially, whose margin is the "rigid integument of the sternum, while the lumen is normally blocked by bulges of the flexible integument which comprises the lining of the vagina." In the set of species having males with long first gonopods, the gonopores of females are paraboloid in outline (Figures 22i-l, 23a-c). Parallels with the other two sets of male gonopod types are less pronounced. Of the intermediate second set, female *C. arcuatus* and *danae* have asymmetrically ovoid gonopores (Figure 22e, f); *exasperatus* has an elongate sinuous gonopore with shelflike overgrowth on the cephalic border (Figure 22g), and *bellicosus* fits into this group (Figure 22h). Females corresponding to the set of males with short first gonopods have gonopores varying from broadly open paraboloid in *C. ornatus* (Figure 22d) to increasingly narrowed openings in *C. gladiator* and *marginatus* (Figure 22b, c), culminating in the narrow transverse slit of *C. similis* (Figure 22a).

MEASUREMENTS

The foregoing discussion shows that measurements must be taken from adults if they are to have systematic usefulness because the young are proportionally different from adults as well as being incomplete for secondary sexual characters. Some species are larger than others and certain proportions are considered useful in keys for identification (Rathbun, 1930; Garth and Stephenson, 1966). Certain populations within species may deviate from the "typical." Initially I thought that analysis of morphometric characters might help to define differences among species as well as among populations within species.

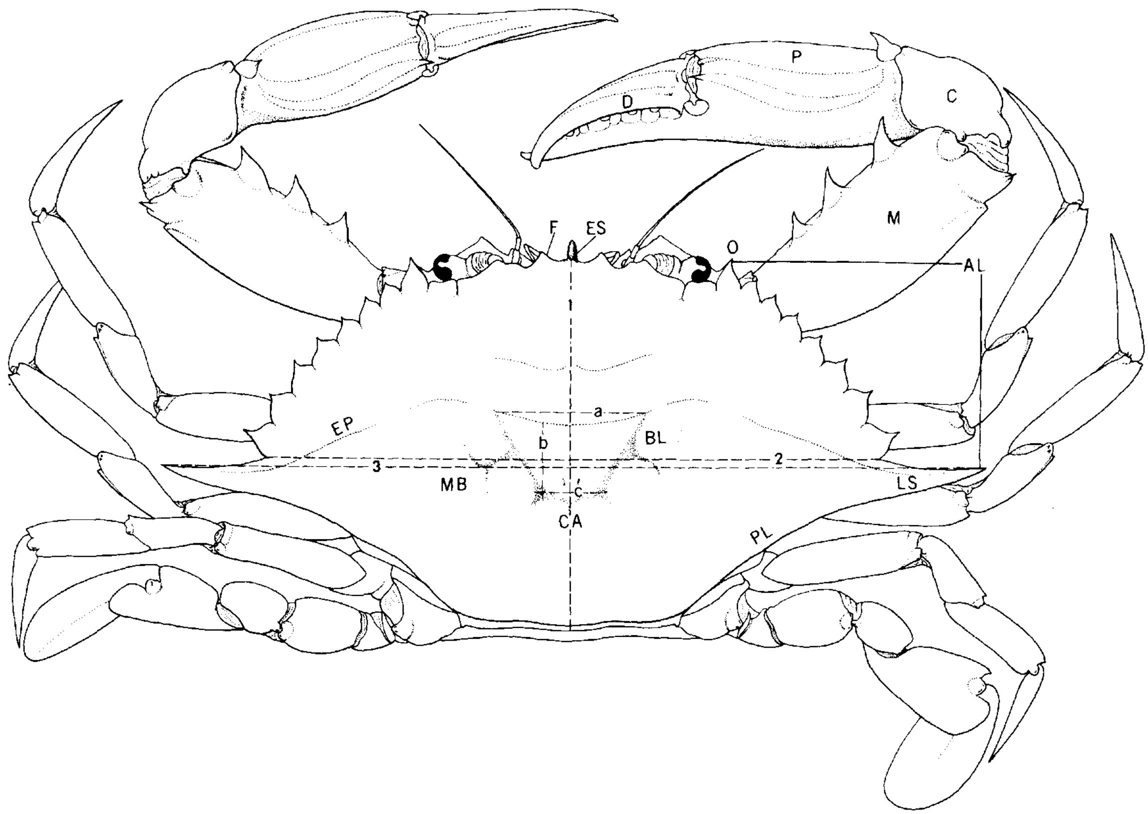

FIGURE 1.—Mature male *Callinectes sapidus* from North Carolina in dorsal view (× 1). Measured features indicated by numbered lines: 1, length; 2, width to base of lateral spines; 3, width including lateral spines; dimensions of metagastric area — a, anterior width, b, length, c, posterior width. Other features included in descriptions: (carapace) F, frontal teeth; O, outer orbital tooth; AL, anterolateral teeth; LS, lateral spine; PL, posterolateral margin; EP, epibranchial line; ES, epistomial spine; MB, mesobranchial area; CA, cardiac area; BL, branchial lobe; (cheliped) M, merus; C, carpus; P, propodus; D, dactyl.

Measurements taken included 18 characters for mature males, 21 for mature females (Figures 1, 2). These characters comprise two sets, one associated with the carapace or general body form, and another with sexual characters. Measurements for both sexes included:

1. Length of carapace including epistomial spine.
2.* Length of carapace excluding epistomial spine.
3.* Width of carapace including lateral spines.
4.* Width of carapace at base of notch between lateral spine and preceding anterolateral tooth.
5.* Width between tips of outer orbital spines (first anterolateral teeth).
6. Width between tips of suborbital spines.
7. Width between tips of lateral interorbital spines.
8.* Maximum height of body.
9.* Anterior width of metagastric area.
10.* Posterior width of metagastric area.
11.* Length of metagastric area.
12.* Angular (lateral) length of metagastric area.

Measurements of elements in the T-shaped male abdomen included:

13. Greatest width of fused segments 3-5.
14. Median length of fused segments 3-5.
15. Median length of narrow segment 6.
16. Narrowest width of narrow segment 6.
17.* Length of telson.
18.* Width of telson.

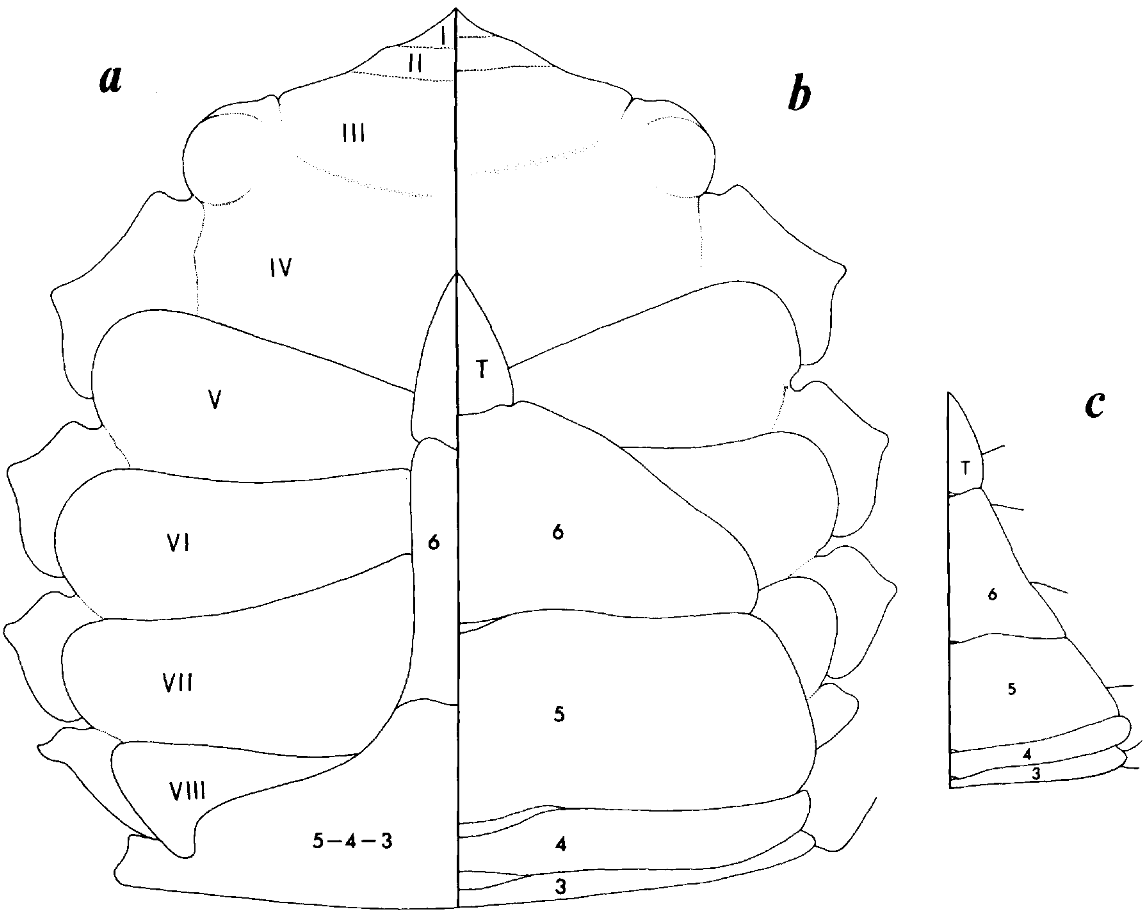

FIGURE 2.—Composite ventral view of thoracic sternites (roman numerals), abdomen (arabic numerals), and telson (T) in situ. **a**, mature male; **b**, mature female; **c**, immature female. Measurements: lengths in midline, widths maximal for structure.

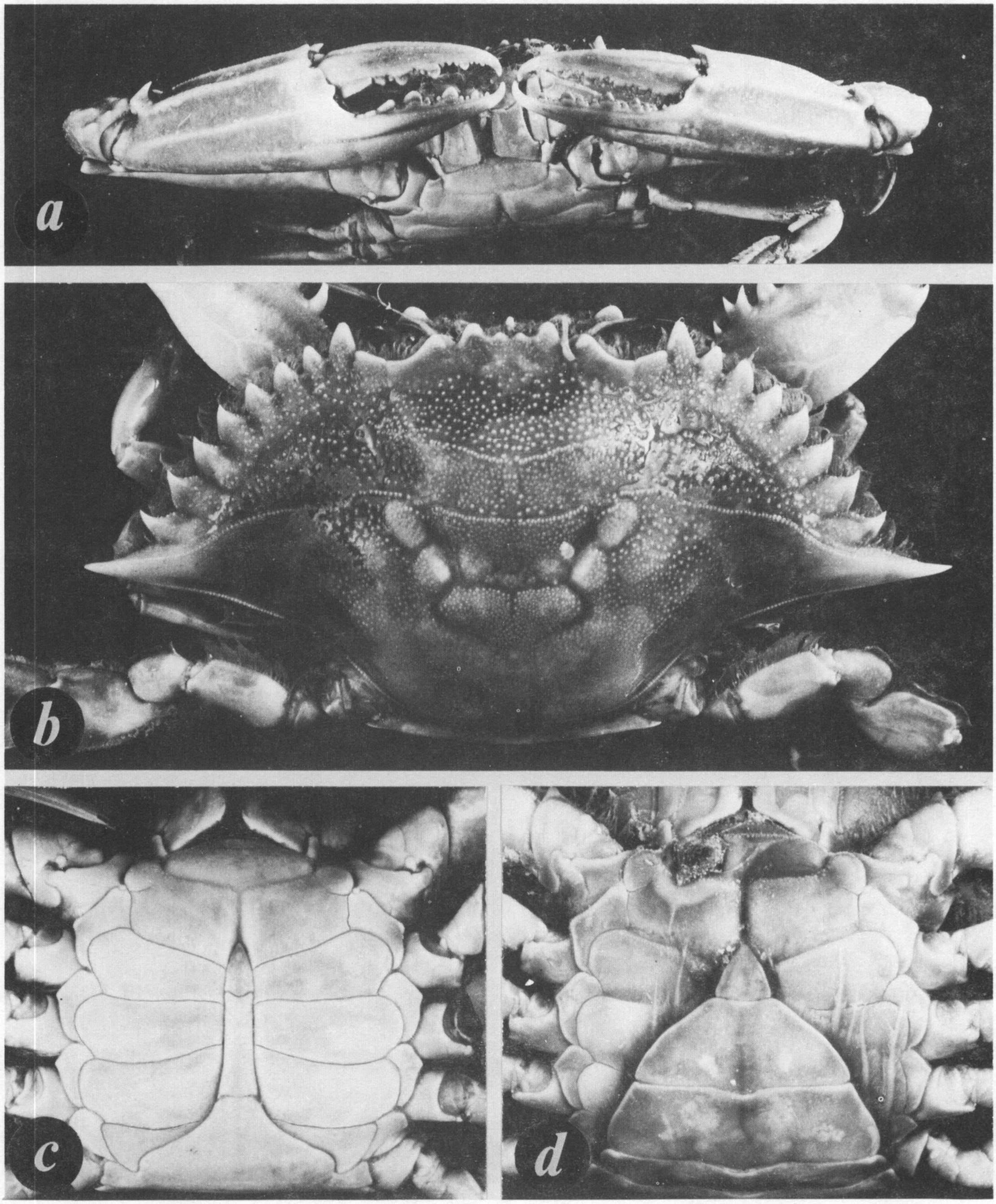

FIGURE 3.—*Callinectes marginatus* (A. Milne Edwards): **a,** chelae in frontal view; **c,** abdomen and sternal area, male, USNM 72351, Salt River Bay, St. Croix, V.I.; **b,** carapace; **d,** abdomen and sternal area, female, USNM 73285, W end San Juan Island near Ft. San Gerónimo, P.R.; **a** × 1; **b** × 1.5; **c** × 1.4; **d** × 1.7.

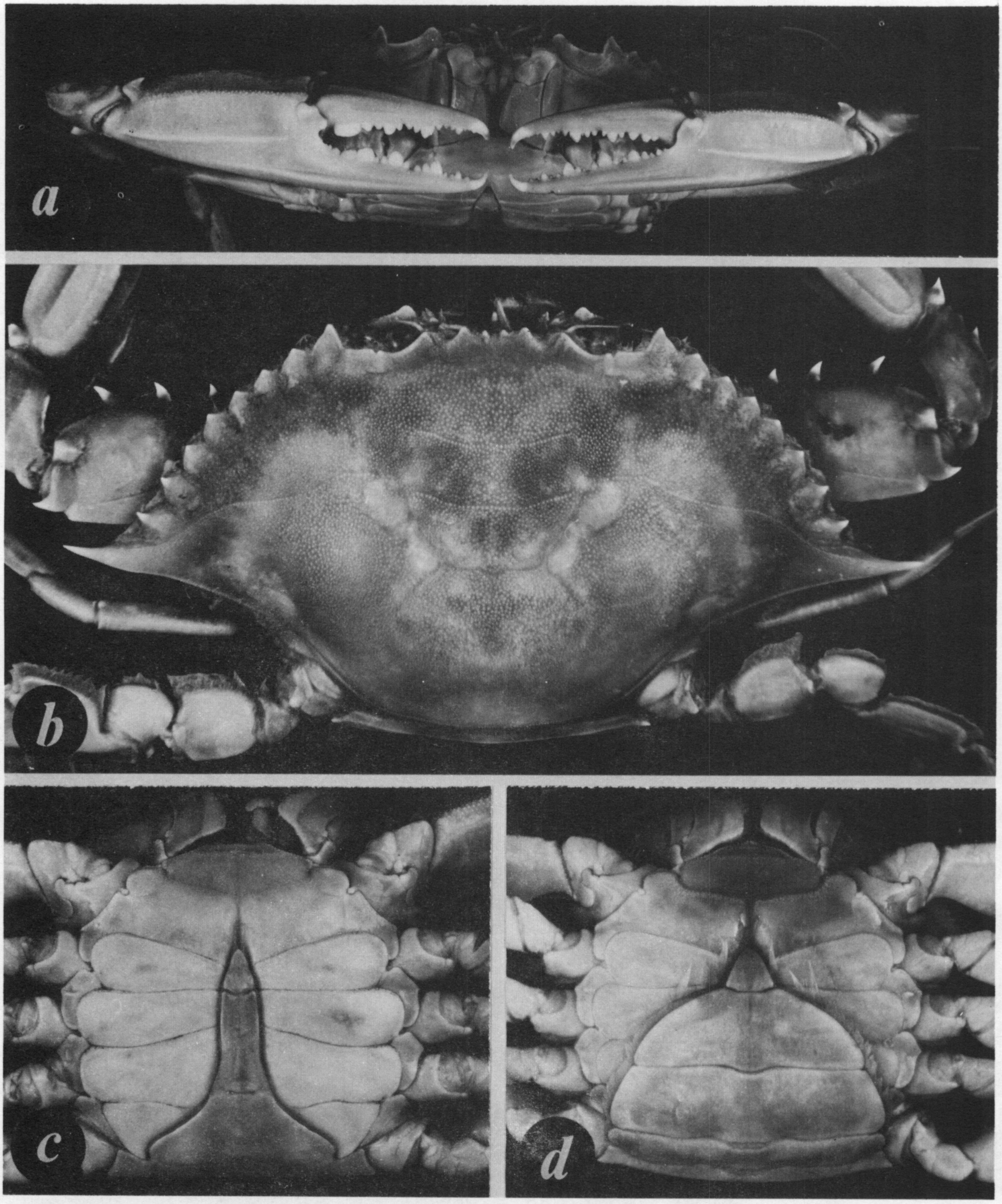

FIGURE 4.—*Callinectes similis* Williams: **a,** chelae in frontal view; **b,** carapace; **c,** abdomen and sternal area, male; **d,** abdomen and sternal area, female; paratypes, UNC-IMS 1556, Beaufort Inlet, Carteret County, N.C.; **a** × 1; **b** × 1.4; **c** × 1.2; **d** × 1.3.