

THE MUD CRAB, *PANOPEUS HERBSTII*, S.L. PARTITION INTO SIX SPECIES (DECAPODA: XANTHIDAE)

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ABSTRACT

The "forms" of the mud crab, *Panopeus herbstii*, s.l., recognized by M. J. Rathbun are rediagnosed as four full species: *P. herbstii*, s.s., from oyster beds of the eastern United States; *P. simpsoni* from that habitat in the Gulf of Mexico; *P. obesus* associated with salt marshes in the Carolinian Province of the southeastern and southern United States; and *P. lacustris* from the intertidal and shallow littoral of the tropical west Atlantic. *Panopeus austrobesus* is newly diagnosed from south of Cabo Frio, Brazil, and *P. meridionalis* from Uruguay. Distinction of these six species is based on morphometry supplemented by color pattern and electrophoretic analysis of hemocyanins. A key for identification is given.

The xanthid crab, *Panopeus herbstii* H. Milne Edwards, s.l. (sensu lato), is recognized as an important member of the American oyster, *Crassostrea virginica* (Gmelin), community. It has been characterized as a selective feeder preferring small oysters over barnacles and large oysters (McDermott and Flower 1952), predatory on oysters and barnacles and potentially the most destructive of mud crabs occurring on New Jersey oyster beds (McDermott 1960), fifth in percent of total biomass on intertidal oyster reefs (Bahr 1976), and the most commonly captured decapod crustacean on Delaware oyster reefs (Maurer and Watling 1973). Menzel and Hopkins (1956) stated that *P. herbstii*, s.l., is a significant oyster predator in Louisiana and that along with *Menippe mercenaria* (Say) it is large enough to kill significant numbers of adult oysters in Florida (Menzel and Nichy 1958). It has also been determined as a consumer of *Cliona celata* Grant, the boring sponge parasitic in oysters (Guida 1976), a detritovore capable of feeding on barnacles and oyster spat (Kendall²), and, though an abundant associate on oyster reefs of Alabama, a commensal and scavenger rather than predator (May 1974). Whetstone and Eversole (1978) found *P. herbstii* to be a predator on hard clams, *Mercenaria mercenaria* (Linné), and Seed (1980) found that both this crab and the blue crab, *Callinectes sapidus* Rathbun, are significant predators on the Atlantic ribbed mussel, *Geukensia* (= *Modiolus*) *demissa* (Dillwyn). McDonald (1982) contrasted the life history pattern of predatory *P. herbstii* with that of the smaller, more omnivorous *Eury-*

panopeus depressus (Smith) in South Carolina. Dame and Vernberg (1982) evaluated the suggestion of Dame and Patten (1981) that mud crabs (e.g., *P. herbstii*) are one of the major controlling components in an oyster reef system, even though the amount of energy flowing through such predators is low in comparison with that moving through other elements of this system, and calculated the energetics of a population of *P. herbstii* in a South Carolina oyster reef on the basis of population density, size structure, standing crop, respiration, and production. The chelae of this and similar species of the family Xanthidae are strikingly adapted for cracking shelled prey, but the exact ecological roles of *Panopeus* species that occur in marine mollusk communities of the eastern and southern United States have been obscured because of imprecise identifications.

Panopeus herbstii has been a species complex from its initial misidentification and illustration as *Cancer panope* by Say (1817-18), through its later description as new in the new genus *Panopeus* by H. Milne Edwards (1834-40), and in a succession of specific and varietal treatments summarized by Rathbun (1930), Williams (1965), Holthuis (1979), and Manning and Holthuis (1981). Rathbun (1930) recognized four primary forms (*typica*, *obesa*, *crassa*, and *simpsoni*) which she believed represented extremes or perhaps environmental types connected by intergrades, but which were not subspecies, although there was a geographic component in her evaluation of material studied. The geographic range of the forms was listed as: form *typica*, Massachusetts to Cedar Keys, Fla.; form *obesa*, South Carolina to southern Brazil; form *crassa*, west Florida to central Brazil; form *simpsoni*, primarily Gulf of Mexico but also South Carolina where it was considered to intergrade with form *typica*.

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²Kendall, D. R. 1974. The ecology of the macrobenthos of a tidal creek, St. Simons Island, Georgia. Unpubl. M.S. Thesis, 212 p. Emory Univ., Atlanta, GA 30322.

Now, three independent investigations which concern elements of this complex have produced results which bear on the status of these forms. The emphasis and method of each study are different, but each employs reference specimens from the crustacean collection of the U.S. National Museum of Natural History. The results of the studies are arranged here as a trilogy. To simplify nomenclature, the first (this paper) presents a taxonomic revision of the complex but rests in part on evidence in the following parts; the second (Sullivan et al. 1983) employs electrophoretic analyses of hemocyanins in the four forms (species) from the Carolinas, the gulf coast of Louisiana and Florida, and the Florida Keys; the third (Reames and Williams 1983) deals with morphological and ecological features of two forms (species) in local populations from southern Alabama.

This paper contains specific diagnoses of these populations partly conceived by Rathbun (1930) through designation as "forms" and includes diagnoses of two additional species from the southern part of the range; it also gives full synonymies of published descriptions with variant spellings of names and critical distributional records, outlines geographic distributions, and provides a key for determination. Some of the older records already included in published synonymies can be associated with nominal species by place of origin.

MATERIALS AND METHODS

Conclusions are based on results presented in Sullivan et al. (1983) and Reames and Williams (1983), on study of specimens in the crustacean collection of the U.S. National Museum of Natural History, Smithsonian Institution (USNM), on type materials in the Yale Peabody Museum (YPM), and photographs of type material in the Museum National d'Histoire Naturelle, Paris (PM).

Form and ornamentation of the carapace have been the main bases for distinguishing "varieties" in this complex in the past, but imprecision in setting limits for the variations led earlier workers to arrive at identities which form improbable species distributions over a broad range of latitude between the northern and southern temperate regions. Factors that contributed to these interpretations include ill-defined "varietal" differences as well as allometric changes, sexual dimorphism, and wear of exoskeletal parts. To increase the number of definitive characters, other features such as shape and ornamentation of the chelipeds and color pattern were employed, although the ranges of variation were increased by these

additions. To avoid the consequent confusion, distributional patterns were outlined by noting the occurrence of "typical" specimens in a large series; once that framework was perceived, the variants could be recognized as such and placed properly.

Mensuration data are treated in two ways. Species diagnoses include proportional measurements, i.e., one measure expressed as a percent of another. Minimum values, maximum values, and arithmetic means are presented in a table to supplement the accounts of each species. In order to test for differences among species, the analysis of covariance (ANCOVA) procedure is used. This procedure tests null hypotheses concerning 1) overall coincidence, 2) equality of slopes, and 3) equality of intercepts of two or more regression equations. If hypothesis 1 is rejected at a prespecified level ($P = 0.05$ in this study), hypotheses 2 and 3 are then tested. If the null hypotheses concerning the slopes or intercepts of three or more groups are rejected, the Newman-Keuls multiple range test (MRT) is used in order to determine which regressions are different from others. It is not uncommon for the ANCOVA procedure to reject a null hypothesis in which the MRT procedure is unable to detect differences. It is generally accepted that the ANCOVA procedure is a more powerful test than the MRT.

Statistical tests were performed on the DEC System 10 Computer³ of the National Marine Fisheries Service, using computer programs written and maintained by Joseph L. Russo for the NMFS Systematics Laboratory.

All statistical procedures and notation used in this investigation follow those presented by Zar (1974), with the exception that the probability associated with the calculated value of the F statistic of the ANCOVA procedure is generated by the computer programs which for the purpose of simplification and clarity is used instead of the calculated value of the F statistic with its associated numerator and denominator degrees of freedom. The independent variable used for all regressions is carapace width.

First pleopods of male crabs were studied with the aid of a light microscope and scanning electron microscope.

Citations in synonymies are limited to descriptive or distributional accounts that can be associated with species. Many references that cannot be assigned to species with certainty are not included.

³Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

SPECIES ACCOUNTS

Panopeus austrobesus new species

Figure 1

Panopaeus herbstii.—Heller 1868:16 (Brazil, locality).

Panopaeus herbstii.—Ortmann 1893b:475 (part).

Panopeus herbstii forma obesa.—Rathbun 1930:336 (part, specimens from south of Cabo Frio, Brazil).

Panopeus herbstii forma crassa.—Rathbun 1930:336 (part, specimens from south of Cabo Frio, Brazil).

Panopeus herbstii.—Coelho and Ramos 1972:190 (part).—Williams 1984:412 (part).

Material examined.—Specimen lots in USNM recorded by Rathbun (1930) under *P. herbstii* (catalog number only) plus material added since that time.

Brazil: 47847, 47851, 59457, 59458, 59459, 59460, 59461, 59462, 59465.—75661. 2M juv.; Ilha Paqueta; W. L. Schmitt, 23 August 1925.—75663. 1F (ovig.); Ilha Governador; W. L. Schmitt, 1 September 1925.—75603. 5 juv.; Santos, on muddy beaches between canals 4 and 5; W. L. Schmitt, 13 September 1925.—75654. 3M, 1F, 3 juv.; Santos estuary; W. L. Schmitt, 13 September 1925.—75653. 1M juv.; Paranagua; W. L. Schmitt, 2 October 1925.—75662. 1M juv.; Paranagua; W. L. Schmitt, 3 October 1925.

Types.—The following are designated and labelled as types deposited in the crustacean collection of the

USNM: 59462. Holotype male, cl 26.5 mm, cw 38.7 mm, Paranagua, Brazil, sandy mud flats, under scattered rocks; W. L. Schmitt, 3 October 1925.—191147. 7M, 2F, same lot of specimens as above and considered as paratypes.

Diagnosis.—Carapace with few transverse lines of granules, slightly coarsened granules on ocular and hepatic regions and along anterolateral slopes (length 64.2-72.9% width, \bar{x} 68.8). Coalesced first and second anterolateral teeth of carapace separated by very shallow notch, broadly rounded second tooth usually but not always exceeded by acute first tooth; remaining teeth outstanding in large adults, less so in smaller specimens, third tooth with rounded to rectilinear tip, fourth swept forward and acute, fifth much smaller, acute and directed anterolaterad; arc drawn along tips of first 4 teeth diverging laterally from arc drawn along bases of notches between teeth. Chelipeds microscopically granular, sometimes more conspicuously so along anterior edge of carpus, granules on outer surface of palm often arranged in obsolescent rugose pattern. Major chela with teeth on fixed finger varied in size, one or more distal to level of basal tooth on dactyl enlarged, with cusps raised above straight line drawn between angle at juncture of finger with anterior margin of palm and tip of finger (= length of fixed finger) (Fig. 2); cusps of teeth on fixed finger tending to be well separated, seldom worn, their external faces sometimes prominent but not noticeably bowed outward from axis of finger.

Measurements in mm.—A set of measurements for length and width of the carapace of this species is summarized in Tables 1 and 2 and graphically represented in Figure 9.

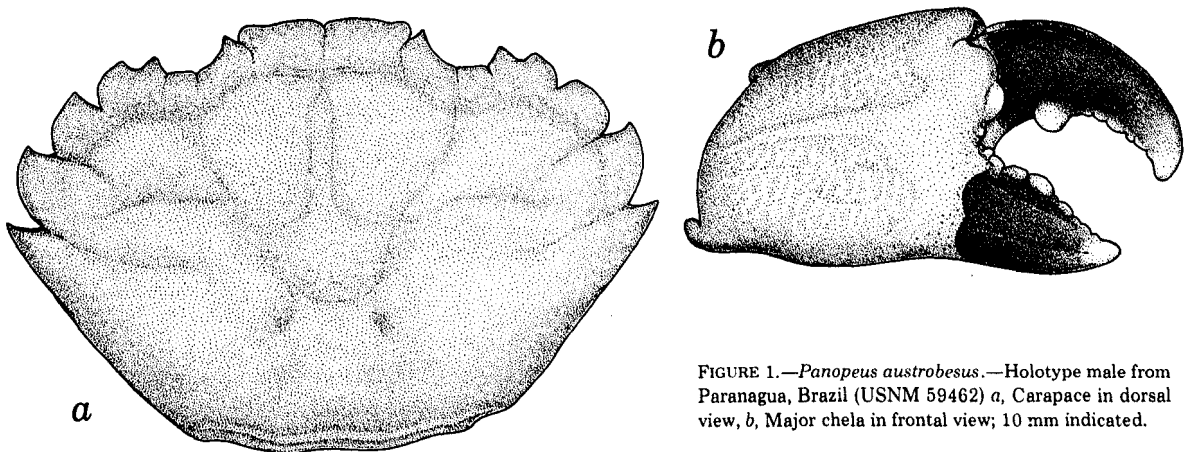


FIGURE 1.—*Panopeus austrobesus*.—Holotype male from Paranagua, Brazil (USNM 59462) a, Carapace in dorsal view, b, Major chela in frontal view; 10 mm indicated.

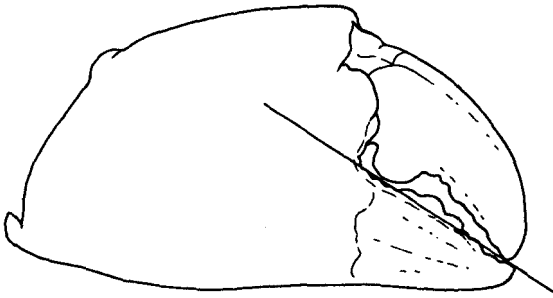


FIGURE 2.—Major chela showing straight line drawn between angle at juncture of fixed finger with anterior margin of palm and tip; cusps of some teeth raised above line in this example (*Panopeus lacustris*).

TABLE 1.—Basic statistics for length percent width of carapace in six species of *Panopeus* from the western Atlantic Ocean.

Species	N	Min.	Max.	Mean	SD
<i>herbstii</i>	50	98.8	77.0	73.2	1.64
<i>simpsoni</i>	50	68.2	77.1	73.5	2.04
<i>meridionalis</i>	7	70.1	74.0	71.7	1.21
<i>obesus</i>	53	59.3	75.5	70.1	2.43
<i>lacustris</i>	57	64.5	78.5	69.3	2.10
<i>austrobesus</i>	44	64.2	72.4	68.8	1.57

TABLE 2.—Linear regression analysis for width (x) and length (y) in millimeters of the carapace for samples of five species of *Panopeus* from the western Atlantic Ocean.

Species	Data pairs	Mean x	Mean y	Min.	Max.	SD	Slope	y intercept	r ²
<i>herbstii</i>	50	26.06	19.04	12.10	46.80	63.075	0.71337	0.44276	0.9952
			19.04	8.70	33.60	33.255			
<i>simpsoni</i>	50	22.21	16.34	11.10	44.00	60.687	0.73741	-0.04489	0.9957
			16.34	7.80	33.50	44.065			
<i>obesus</i>	53	31.96	22.36	15.40	50.90	77.889	0.68597	0.43766	0.9893
			22.36	9.90	36.30	37.047			
<i>lacustris</i>	57	37.90	26.08	14.80	56.80	157.590	0.65622	1.20575	0.9953
			26.08	10.60	38.80	68.181			
<i>austrobesus</i>	44	30.81	21.14	18.50	51.30	56.659	0.63977	1.41792	0.9924
			21.14	13.20	35.10	23.383			

Color.—Occasionally with random spots on external side of palms.

Known range.—Region of Rio de Janeiro, Brazil, to Florianopolis, Brazil (and probably southward).

Name.—The specific name is derived from the Latin "australis," southern, and "obesus," in reference to its similarity to *P. obesus*.

Remarks.—*Panopeus austrobesus* has carapace dimensions and outstanding anterolateral teeth that almost exactly match those of *P. lacustris*, although

areolations of the carapace and its transverse lines of granules are less distinct than in that species. The chelipeds, however, are more smoothly granulated than in *P. lacustris*, recalling the surface of chelae in the *simpsoni-herbstii* group; but the tooth pattern of the fixed finger has a striking similarity to that of *P. obesus*.

***Panopeus herbstii* H. Milne Edwards, s.s.**

Figure 3

Cancer panope.—Say 1817:58, pl. 4, fig. 3 (misidentified).

Panopeus herbstii H. Milne Edwards 1834:403.—Lucas 1840:90.—Gibbes 1845:63, 69.—1850b:175 (part, not Key West material).—Leidy 1855:149.—Smith 1869a:276 (part, the South Carolina and E. Florida material).—1869b:34 (part, list).—Coues 1871:120.—Kingsley 1878:318 [3] (part).—1880:393 (part).—A. Milne Edwards 1878-1880:308 (part), pl. 27, fig. 2, 2a.—R. Rathbun 1884:772 (part).—Benedict and Rathbun

1891:358 (part), pl. XIX, fig. 1, pl. XXIII, figs. 10(?), 12.—Rathbun 1905:6.—1930:335 (part, *forma typica*), text figs. 52, 53; pl. 156, figs. 1-2.—Fowler 1912:404, pls. 122-123.—Hay and Shore 1918:437 (part), pl. XXXIV, fig. 9.—Lunz 1937:13 (part).—McDermott and Flower 1952 2:48-49.—Williams 1965:196 (part), fig. 180.—1974:34, fig. 97 (key).—1984:412, fig. 326 (part).—Williams and Wigley 1977:11 (part, distribution).—Gosner 1971:543, 550 (key), fig. 21.61A.—Van Engel and Sandifer 1972:160 (list).—Felder 1973:pl. 9, fig. 21.—Young 1978:182 (list).—Holthuis 1979:159 (selection

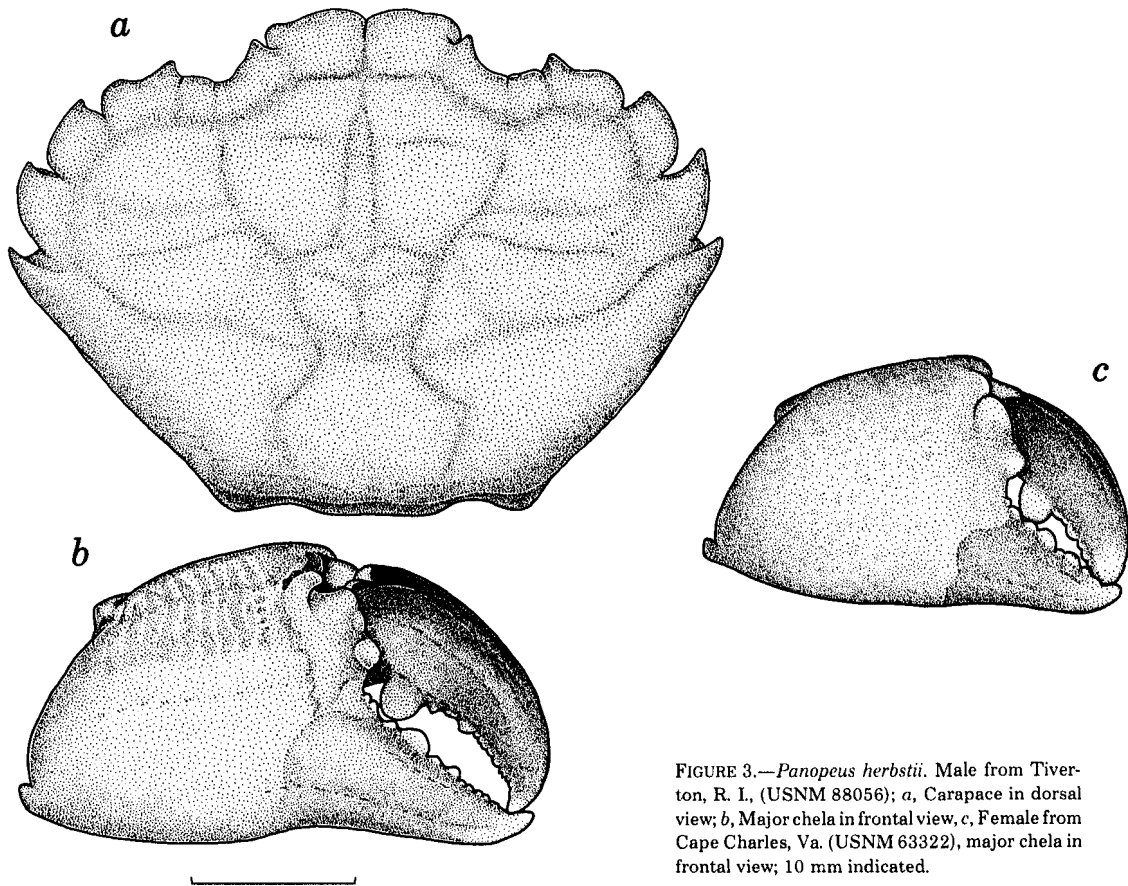


FIGURE 3.—*Panopeus herbstii*. Male from Tiverton, R. I. (USNM 88056); a, Carapace in dorsal view; b, Major chela in frontal view, c, Female from Cape Charles, Va. (USNM 63322), major chela in frontal view; 10 mm indicated.

of lectotype).

Panopeus herbstii.—DeKay 1844:5.—Ryan 1956:147 (part, in eastern USA) pl. 1, fig. C; text figs. 3, 4B, 5B, 9A.—McDermott 1960:201-210, fig. 1.—Schwartz and Cargo 1960:201-203.—Wass 1961:XII-14 (list).—1963:44 (list).—1965:41 (list).—Smith 1964:119 (key).—Maurer and Watling 1973:161, 179.

Panopeus Herbstii.—Gibbes 1845:69 (? no locality).—1850a:23.—Stimpson 1860:444.—Smith 1873:547.—Verrill et al. 1873:547 (part).

Panopaeus herbstii.—Ortmann 1893a:57 (part).

Eupanopeus herbstii.—Rathbun 1900b:138 (key, part).—1905:6.

Panopeus simpsoni.—Rathbun 1930:338-339 (part, material from Virginia to South Carolina).

Panopeus (Eupanopeus) herbstii.—Miner 1950:522, pl. 167, colored pl. XII, 5.

Material examined.—Lots of specimens in USNM recorded by Rathbun (1930) under *P. herbstii*

(catalog numbers only) plus material added since that time.

Massachusetts: 173575. 1M; Sippewisset Marsh, West Falmouth, 41°34'45"N, 70°38'22"W, 1 m, muddy sand; C. Wheeler, 28 June 1979.

Rhode Island: 4539.—88056. 7M, 4F; Sakonnet River, N side of Stone Bridge, Tiverton; F. A. Chace, Jr., 4 September 1948.

Connecticut: 15690.

New Jersey: 75626. 1F (ovig.); Mullica River; H. G. Richards, 6 July 1931.—75624. 1F; Thorofare, Atlantic City; H. G. Richards, 14 August 1931.—75625. 2M; Great Egg River; H. G. Richards, 13 August 1931.—76154. 1M; Cape May Point; H. G. Richards, 20 March 1932.—63321. 2 juv.; Prissywick Shoal off Cape May; H. G. Richards.

Delaware: 191148. 2M, 1F; Wreck N Roosevelt Inlet and Nantauxent Point; W. Amos, 1952-56.

Maryland: 56266.

Virginia: 22328, 48850, 56267, 56268, 56386, 56837, 57139.—75595. 3M, 1F; Smith's I., from

oyster bed 0.5 mi S of light at low tide; J. P. E. Morrison, 6 July 1935.—191149. 1F (ovig.); Wachapreague; 24 July 1943.—63322. 1F; Cape Charles, near wharf; H. G. Richards.—63323. 1F (juv.); Cape Charles; H. G. Richards.—63324. 2F; Cape Charles, near wharf; H. G. Richards.—74600. 5M; York River, 6 ft; J. B. Engle, U.S. Bur. Fish., 21 October 1936.—75628. 1F; Yorktown; J. B. Engle, U.S. Bur. Fish.—75668. 1F; Yorktown; J. B. Engle, U.S. Bur. Fish.

North Carolina: 62538, 62539, 62540.—60607. 1M; Hatteras; A. J. Poole and R. Kellogg, May 1927.—191172. 2M; Pivers I., Beaufort; J. B. Sullivan, 10 July 1978.—84428. 2M; Fort Macon, Beaufort, under stones in muddy zone just above low water on breakwater; T. A. and A. Stephenson, Stn. BM(N)39, 1947.

South Carolina: 15726, 15741, 15762, 15780, 15782, 26150, 42881, 45502, 51022, 56265, 59938.—75667. 1M; Dewees I.; G. R. Lunz, Jr., 15 May 1934.

Florida: 56838.—99909. 2F; Bridge over Matanzas River, Crescent Beach; D. K. Caldwell et al., 1 December 1954.—170017. 1M; Sebastian Inlet, Indian River Co.; on sabellariid reef S side under bridge, intertidal; R. H. Gore, 7 May 1974.

Locality uncertain: 56840. 2F; east coast of North America; Boston Society of Natural History.—75596. 1M, 5F (1 ovig.); O. Bryant, Boston Soc. Nat. Hist.

Diagnosis.—Coalesced first and second anterolateral teeth of carapace separated by shallow rounded notch, second tooth broader than but not so prominent as first tooth; third and fourth anterolateral teeth curved anteriorly; fifth tooth much smaller than fourth, acute and swept forward or hooked anteriorly. Carapace length 66.8–77.0% width, \bar{x} 73.2. Chelipeds superficially smooth but actually finely granulate on upper surface of carpus; lower outer surface of palms light colored (pink, buff, or yellowish, rarely mottled reddish); major chela with cusps of teeth on fixed finger usually either reaching or falling below straight line drawn between angle at juncture of finger with anterior margin of palm and tip of finger (= length of fixed finger); anterior margin of palm with distance between crest at base of dactyl and tip of condylar tooth lateral to base of dactyl 0.70 or less length of fixed finger.

Measurements in mm.—A set of measurements for length and width of the carapace of this species is summarized in Tables 1 and 2 and graphically represented in Figure 9.

Color.—Dull olive, brown-green, dirty gray or slate color, sutures between regions sometimes lighter, and some tendency to variegated dark pattern on lighter background. Chelipeds darker with variegation coarse on upper parts, sometimes spotted claret brown, blotching extending about halfway down sides of articles, lower half and underparts light; fingers black. Third maxillipeds of males and about half of females with red or burgundy spot near base of inner surface of ischium. (Specimens from Beaufort, N.C.; Hay and Shore 1918; Rathbun 1930.)

Type-locality.—“Inhabits oyster beds, &c... often found on oysters (*O. virginica*) in our markets” [by implication the eastern United States] (Say 1817:58). Holthuis's (1979) selection of the specimen figured by Say (1817, pl. 4, fig. 3) as the lectotype for *P. herbstii* restricts the nominal species to the common mud crab occurring on oyster bars of the eastern United States.

Known range.—The known geographic range of this species, represented by the material listed above, is shallow intertidal and subtidal waters of the eastern United States from Boston Harbor, Mass., to Indian River County, southeastern Florida.

Remarks.—See general discussion below.

Panopeus lacustris Desbonne

Figure 4

Panopeus lacustris Desbonne 1867:28.

Panopeus herbstii.—Gibbes 1850b:176 (part, Key West material).—Smith 1869a:276 (part, the Bahamian material).—Kingsley 1880:393 (part).—Rathbun 1884:772 (part).—Benedict and Rathbun 1891:358 (part, the Bermuda, Caribbean, and Brazilian material).—Young 1900:132.—Rathbun 1924:14.—Chace 1940:34.—Chace and Hobbs 1969:154, figs. 46c, 47.—Holthuis 1959:207.—Edmondson 1962:277, fig. 20c (?).—Coelho 1966:163 (habitat).—1970:53 (habitat).—Coelho and Ramos 1972:190 (part).—Fausto Filho 1966:33 (occurrence).—Bonnely de Calventi 1974:27 (list).—Markham and McDermott 1981:1273 (list).—Williams 1984:412 (part).

Panopeus herbstii.—Smith 1869b:34 (part, listing).—von Martens 1872:89.—Verrill et al. 1874:547 (part).—A. Milne Edwards 1880:13 (Brazil locality).

Panopeus herbstii var. *obesus* Smith 1869a:278 (part, the Aspinwall material).

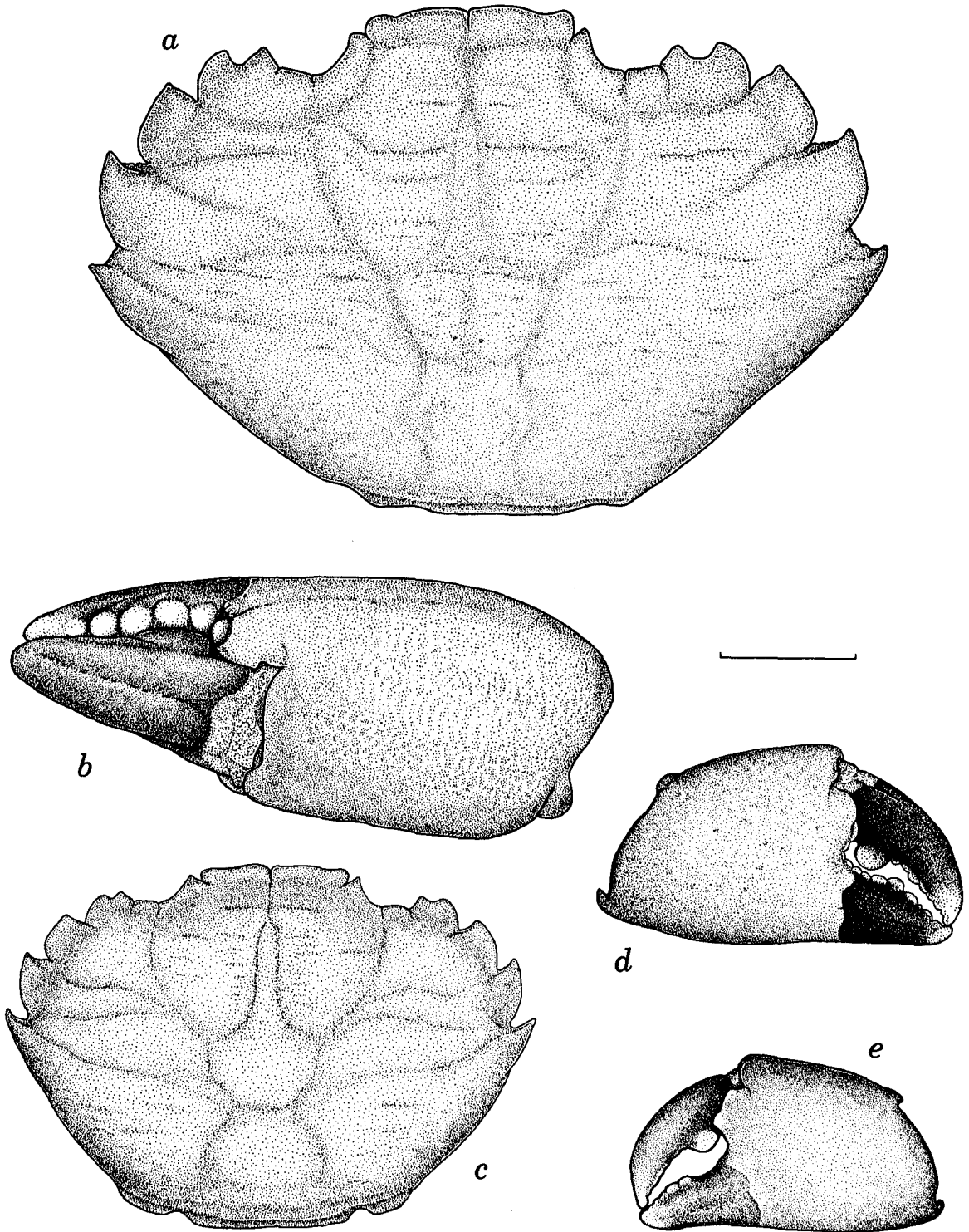


FIGURE 4.—*Panopeus lacustris*. Male from southern Florida (USNM 75643); a, Carapace in dorsal view; b, Major chela in oblique dorsal view showing broadened "molar" teeth on fixed finger. Female from St. Croix, W.I.; c, Carapace in dorsal view; d, Major chela in frontal view. e, Male from Panama (YPM 470), major (left) chela in frontal view, teeth of fixed finger worn. 10 mm indicated.

Panopeus Herbstii granulatus A. Milne Edwards 1880:309.

Panopeus crassus A. Milne Edwards 1880:313, pl. 57, figs. 1, 1a; 2, 2a.—Benedict and Rathbun 1891:383.

Panopeus herbstii granulatus.—Benedict and Rathbun 1891:383.—Young 1900:134.

Panopaeus herbstii.—Ortmann 1893a:57 (part).—1893b:475 (part).

Eurypanopeus herbstii.—Rathbun 1897:18 (listing).

Eupanopeus herbstii.—Rathbun 1898:273.—1900a:140.—1901:28.

Panopeus herbstii obesus.—Young 1900:134.

Eupanopeus Herbstii, var. or subspecies, *minax* Verrill 1908:348, text fig. 15; pl. 15, fig. 2.

Panopeus herbstii [sic].—Gundlach et al. 1917:564, fig. 16.

Panopeus herbstii forma crassa.—Rathbun 1930:336, pl. 157, fig. 3.—1933:61, fig. 53.

Panopeus herbstii.—Coelho 1971:283 (habitat).

Material examined.—Lots of specimens in USNM recorded by Rathbun (1930) under *P. herbstii* (catalogue numbers only) plus material added since that time.

Bermuda: 25825, 43046.—94239. 1M; Harrington Sound; T. A. Stephenson, Stn. BRH-21.—94240. 2M; Ferry Reach; T. A. Stephenson, Stn. BRM-3.—143596. 2M; Riddells Bay, algal mat; J. E. Pearson, July 1972.

Florida: 2077, 9254, 9296, 15412, 15419, 59456, 59937, 61122, 62541, 62542, 62544.—170016. 1M; Sebastian Inlet, Indian River Co., on sabellariid reef S side under bridge, intertidal; 19 June 1974.—170015. 1M, 1 juv.; Sebastian Inlet, Indian River Co., on sabellariid reef S side under bridge, intertidal; R. H. Gore, 1 November 1974.—170014. 1M, 2 juv.; Sebastian Inlet, Indian River Co., on sabellariid reef S side under bridge, intertidal; R. H. Gore, 9 December 1975.—170013. 1F; Link Port, Indian River, St. Lucie Co., intertidal; R. H. Gore, 8 December 1975.—170018. 1M, 3F (2 ovig.); Ft. Pierce, Jim Island mud flats in grass beds, intertidal; R. H. Gore, 26 June 1972.—75643. 1M; vicinity of Coral Gables; J. F. W. Pearson.—75656. 1F; vicinity of Coral Gables; J. F. W. Pearson.—191150. 1M; Big Pine Key, southeast point, beach rock, littoral fringe; Gosner, Stn. 257, 16 January 1968.—75613. 1F; Key West; U.S. Bur. Fish.—75614. 1F; Key West; U.S. Bur. Fish.—75645. 1M; Key West; U.S. Bur. Fish.—75649. 1M, 2F; Key West; U.S. Bur. Fish.—75655. 1F (ovig.); Key West; U.S. Bur. Fish.—75611. 1M; Marquesas Key; A. S. Pearse, 11 August 1930.—75642. 1M; Tortugas; W. L. Schmitt,

1932.—75644. 1M, 1F; Tortugas, from *Porites* clumps, low tide after supper; W. L. Schmitt, 2 July 1931.—72270. 1M juv.; Long Key, Tortugas; W. L. Schmitt, 30 July 1924.—75594. 1F; Bush Key, Tortugas, N point; W. L. Schmitt, 18 June 1932.—75622. 1M; Bush Key, Tortugas; W. L. Schmitt, 27 July 1931.—75659. 1M; W side of Bush Key Reef, Tortugas; W. L. Schmitt, 20 August 1924.—191151. 1M, 2F; Bush Key; W. L. Schmitt, 24 August 1924.—71026. 2F; Fort Jefferson, Tortugas; under coral debris at and near top of moat; A. S. Pearse, 21 June 1931.—75610. 1M; Fort Jefferson, Tortugas; Dexter, 4 August 1930.—75608. 2M, 2F (1 ovig.); Cook Key (west coast); Springer, 13 March 1936.—75615. 1M, 1F; Caxambas-Marco Cut, not bicolored in life; Springer, 13 March 1936.—75607. 1F(juv.); Caxambas-Marco Cut near Coon Key; Springer, 13 March 1936.—75609. 1F, 1 juv.; Marco-Caxambas Cut near Coon Key; Springer, 13 March 1936.

East Coast of United States: 75597. 1M, 1F; Univ. Iowa.

Mexico: 191152. 1M; Beach Champoton, Campeche; ASP, 13 July 1932.

Bahamas: 20710, 23829, 57008.—88658. 2F; Bimini; A. S. Pearse, 16 October 1948.—88659. 2 juv.; Bimini; A. S. Pearse, 29 October 1948.—75658. 1M; Spanish Wells; Univ. Iowa.

Cuba: 24329, 48551, 48553, 48559, 53343, 58393, 59896.—99955. 1F; Laguna Choco, E of Xanadu, Hicacos Pen., Matanzas Prov.; W. L. Schmitt, 24-25 January 1957.

Jamaica: 15654, 19591, 41750, 42933, 59472, 61366, 61587, 62537, 62543.—72777. 1F, 1 juv.; the Palisades, Kingston Harbor; W. G. Lynn, 1 July 1936.

Puerto Rico: 24246, 24266, 24268.

Virgin Islands: 72358. 1M, 2F, 1 juv.; St. Croix, Fairplain str. below bridge, under stones in gravelly bank; H. A. Beatty, 1935-36.—73327. 1M, 2F; St. Croix, Salt River Lagoon; Smithsonian-Hartford Exped. 10 April 1937.—75641. 1F (ovig.); St. Croix, on mangroves bordering Shoys Lagoon; H. A. Beatty, 1937.—75646. 1M, 2F (ovig.); St. Croix; H. A. Beatty.—75606. 1M (juv.); St. Croix, on mangroves bordering Shoys Lagoon; H. A. Beatty.—75045. 3M, 3F; Mangrove I., Salt River, St. Croix; W. L. Schmitt, 10 April 1937.

Leeward Islands: 58037.—75619. 1M; Pillars of Hercules, Antigua; Barbados-Antigua Exped. Univ. Iowa, 1918.

Barbados: 58036.

Trinidad: 7640, 756759, 57012.—137742. 3M, 2F; Caroni Swamp, Colorite Swamp, mangrove roots; J. Stanley, 5 January 1970.

Dutch West Indies: 7585, 42979, 56889.—191173. 1M; Netherlands Antilles; Gosner, September 1968.

Panama: 44180, 44181, 59319.—191153. 1M; Laguna de Chirigui; F. Richardson, 2 April 1936.—139587. 2F; Canal Zone, Ft. Sherman, Shimmey Beach, intertidal; L. G. Abele, 8 February 1969.—139588. 1M; Canal Zone, Galeta Island, small lagoon; L. G. Abele, 14 May 1969.—139589. 1F; Canal Zone, Galeta Island, mangrove swamp, intertidal; L. G. Abele, 24 May 1969.—139590. 2M; Canal Zone, Galeta Island, mangrove swamp, intertidal; L. G. Abele, 14 July 1969.—153994. 7M, 4F; Canal Zone, Galeta Island, mangrove swamp; L. G. Abele, 14 July 1969.—153995. 3M; Canal Zone; L. G. Abele, 1971.—155266. 3M, 1F (ovig.); Canal Zone, Coco Solo Airfield, along seawall, 0.5 m; L. G. Abele, 4 January 1969.—155269. 3M, 1F; Canal Zone, Galeta Island, reef next to lab.; L. G. Abele, 11 March 1969.—155267. 1F (ovig.); Canal Zone, Galeta Island, reef next to lab.; L. G. Abele, 11 March 1969.—155270. 1M; Canal Zone, Galeta Island, mangroves; L. G. Abele, 14 July 1969.

Colombia: 7562, 25655.

Brazil: 25732, 25733, 25734, 40584, 40585.—75553. 1M; Recife, Pernambuco; von Ihering.—75593. 1F, 2 juv.; Bom Sucesso, Minas Geraes; D. Cochran.—90367. 1F; Ilha do Fundito, 22°50'30"S, 43°14'W, Rio de Janeiro; L. de Oliveira, 15 January 1947.

Hawaii: 81729. 1M, 1F; Pearl Harbor, Oahu; C. H. Edmondson, 1940.—95605. 1M; Maunaloa Bay, Oahu, sand flats; C. H. Edmondson, 6 February 1953.—99169. 1F; Pearl Harbor, Oahu; C. E. Cutress, 22 April 1950.

YPM 470. 1M, 1F; Aspinwall [= Colón, Panama].

Diagnosis.—Carapace with transverse lines of granules, coarse granules on ocular and hepatic regions and along anterolateral slopes, length 64.5–78.5% width, \bar{x} 69.3. Coalesced first and second teeth of carapace often separated by deep rounded notch, second broader than first but tips almost equally prominent (variable in form); remaining teeth outstanding (especially in adults), tips usually rectangular to acute; arc drawn along tips of first four teeth diverging laterally from arc drawn along base of notches between teeth. Chelipeds bearing distinct closely crowded granules, especially along anterior edge of carpus and on upper and outer surface of palm (often in obsolescent rugose pattern); distinct reticulate pattern of color on outer surface of palm, usually continued over its lower half, and accented with random scatter of spots, mainly in upper half

(may be faded but evident after long preservation). Major chela with teeth on fixed finger varied in size, a group distal to level of basal tooth on dactyl enlarged with cusps raised above straight line drawn between angle at juncture of finger with anterior margin of palm and tip of finger (= length of fixed finger); cusps in proximal "molar area" of fixed finger broad, often impacted, and worn severely, their external faces and external side of finger swollen, flared, or bowed outward from axis of finger.

Measurements in mm.—A set of measurements for length and width of the carapace of this species is summarized in Tables 1 and 2 and graphically represented in Figure 9.

Color.—Usually lighter in color than russet colored *P. obesus*, often grayish dorsally, cream ventrally and on lower parts of chelae. Reticulate pattern on outer surface of chelae as in *P. obesus* and sometimes with scattered spots on this surface.

Type-locality.—The lagoons of Guadeloupe, hiding under rocks.

Known range.—The known geographic range of this species, represented by material listed above, is shallow and subtidal waters from Bermuda and extreme southern Florida, through the West Indies, and along the continental margin of the Caribbean Sea and South America to Cabo Frio, Brazil. The species has been introduced in Hawaii, and, according to a report by Edmondson (1962), apparently has been known on the California coast for a number of years. It is often associated with mangroves as well as coarse substrates.

Remarks.—Desbonne's (1867) description clearly applies to what is here recognized as a single species of this *Panopeus* complex in the tropical western Atlantic, and his long suppressed name, rather than A. Milne Edwards' *P. crassus*, has priority.

The large series of study specimens in the USNM was augmented by excellent photographs of a syntype male of *Panopeus crassus* A. Milne Edwards from Bahia which was kindly supplied to me from the Museum National d'Histoire Naturelle by M. J. Forest. Parenthetically, measurements for a male given in the original description (cl 36 mm, cw 65 mm) of *P. crassus* depart considerably from the shape of any specimens measured by me, but the dimensions of the carapace of the figured male correspond to those of the male from Bahia in the Paris Museum (cl 36 mm, cw 56 mm), suggesting that digits in measure-

ment of width recorded in the original text were transposed.

Smith's (1869a) syntypes of *Panopeus herbstii* var. *obesus* from Aspinwall are actually *P. lacustris*, a male, cl 21.3, cw 30.2, with left major chela, and an immature female, cl 16.1, cw 23.2, with right major chela. The carapace of each specimen, while somewhat inflated, shows the slight surface sculpture, transverse lines of granules, granular frontal and anterolateral slopes characteristic of *P. lacustris*, and most noticeably its outstanding curved but pointed anterolateral teeth, the third and fourth being most characteristic; the first and second tooth are coalesced but well separated by a moderate notch, the rather acute first tooth being one-fourth to one-third as wide as the much more rounded second and slightly exceeding it in each case. The front is fairly prominent in both specimens and granular along its edge.

In both specimens, the molar teeth of the crushing chela are strong, coalesced, broadened, raised, bowed laterally from the longitudinal axis of the finger, and opposed by a well-developed dactylar tooth. In both specimens, the molar area of the fixed finger is worn, noticeably so in the male. The minor chela of the female is typical for a specimen of this size, but that of the male is relatively slender, the fingers somewhat more decurved than normal, and the tip of the dactyl broken off. The right third walking leg of the female is missing and the left first and right third to fifth walking legs missing in the male.

No color is evident except for the slightly brownish gray fingers of the chelae, with their lighter tips and tooth cusps, but the fingers of the regenerated minor

chela of the male are darker than others. There is faint indication of the reticulate color pattern on the large chela of each specimen.

Other remarks are given in the general discussion below.

Panopeus meridionalis new species

Figure 5

Material examined.—USNM 99846, holotype male, cl 19.4 mm, cw 26.9 mm, Montevideo and Punta Carretas, rock coast of Rio de la Plata, Uruguay; C. S. Carbonell, 1955.—191154. 2M, 4F; same lot of specimens as above and considered as paratypes.

Diagnosis.—Carapace relatively narrow, length 70.1–74.0% width, \bar{x} 71.7. Coalesced first and second anterolateral teeth usually separated by very shallow notch, tip of acute first tooth exceeding that of second; third and fourth teeth strongly curved forward, acute, anterior margin of each concave; fifth much smaller than fourth, slightly curved forward. Chelipeds finely granulate on upper surface of carpus and palm; lower outer surface of palms appearing light colored in preserved material. Major chela with teeth on fixed finger varied in size, one or more teeth on fixed finger distal to level of basal tooth on dactyl enlarged, with cusps raised above straight line drawn between angle at juncture of finger with anterior margin of palm and tip (= length of fixed finger); cusps of teeth on fixed finger rather well separated, not broad, seldom worn, their external faces not flared or bowed outward but aligned along axis of finger.

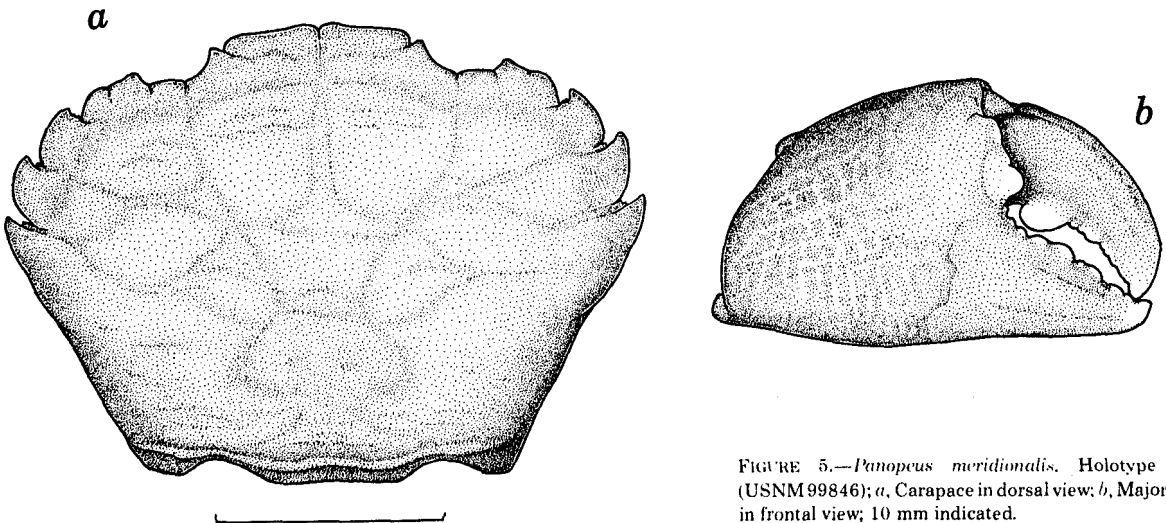


FIGURE 5.—*Panopeus meridionalis*. Holotype male (USNM 99846); a, Carapace in dorsal view; b, Major chela in frontal view; 10 mm indicated.

Measurements in mm.—A set of measurements for length and width of the carapace of this species is summarized in Tables 1 and 2 and graphically represented in Figure 9.

Color.—Third maxillipeds of males with red spot near base of inner surface of ischium. No other reliable color pattern is evident in preserved material.

Known range.—The only specimens known are those from the type-locality.

Name.—The specific name is derived from the Latin "meridionalis" southern, in reference to the extreme southern distribution.

Remarks.—This species has acute, forwardly swept anterolateral teeth that recall those of *P. simpsoni* from the Gulf of Mexico. Granulation of the chelipeds

is smooth as in *P. simpsoni* and *P. herbstii*, but the tooth arrangement on the fixed finger of the major chela is closer to that of *P. obesus* or *P. austrobesus*. *Panopeus meridionalis* thus occupies an intermediate position between the *herbstii-simpsoni* group and the *obesus, austrobesus, lacustris* group of this genus.

Panopeus obesus Smith, new rank

Figures 6, 7

Panopeus herbstii var. *obesus* Smith 1869a:278 (part, the Egmont Key specimen).—Coues 1871:120.—Kingsley 1878:318 [3] (part).

Panopeus herbstii.—Kingsley 1880:437 (part).—Rathbun 1884:772 (part).—Hay and Shore 1918:437 (part).—Lunz 1937:13 (part).—Williams 1965:196 (part).—1984:412 (part).—Felder 1973:69 (part, key).—Powers 1977:102 (part, notes).

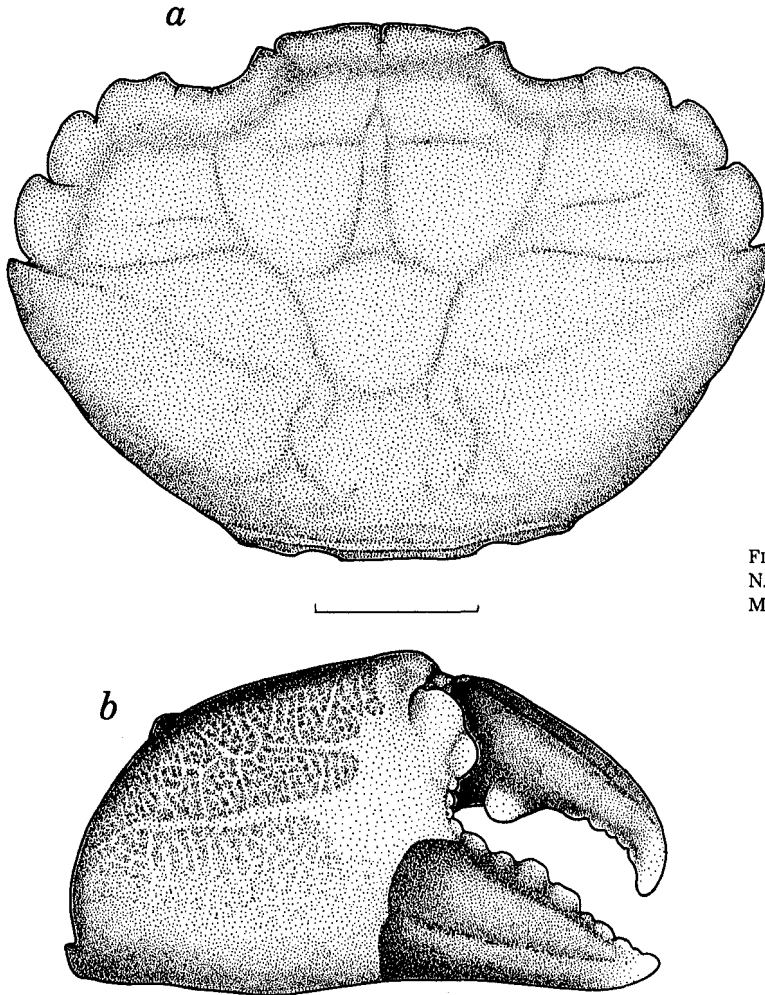


FIGURE 6.—*Panopeus obesus*. Male from Beaufort, N.C. (USNM 191157); a, Carapace in dorsal view; b, Major chela in frontal view; 10 mm indicated.

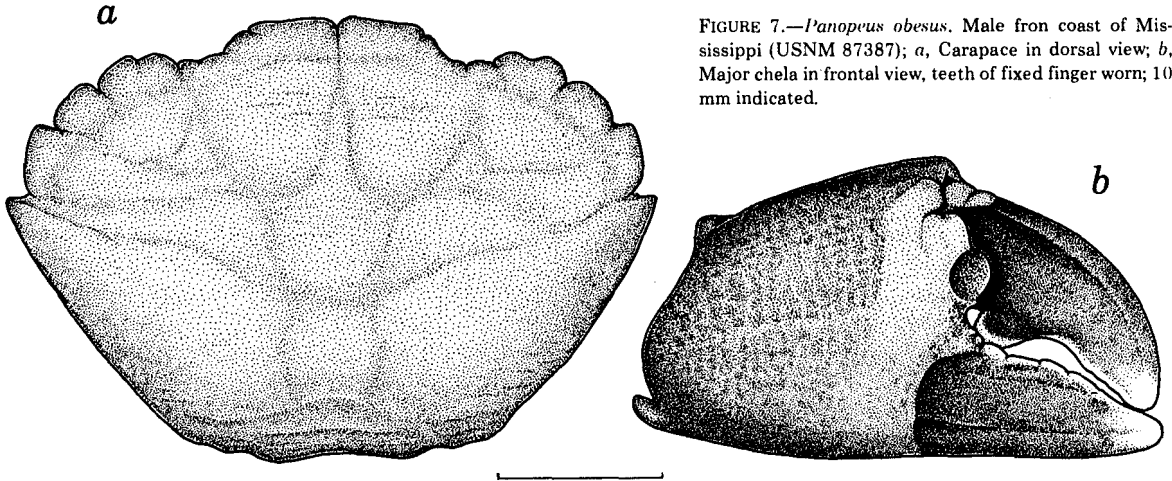


FIGURE 7.—*Panopeus obesus*. Male from coast of Mississippi (USNM 87387); a, Carapace in dorsal view; b, Major chela in frontal view, teeth of fixed finger worn; 10 mm indicated.

Panopeus Herbstii obesus (variety).—A Milne Edwards 1880:309.

Panopeus herbstii forma obesa.—Rathbun 1930:335, pl. 156, fig. 3.

Panopeus herbstii forma obesa.—Behre 1950:24 (list).

Panopeus herbstii forma obessa Heard 1982:50, fig. 56a-c.

Material examined.—YPM 901. Lectotype F; Egmont Key, Fla.; col. E. Jewett.

Specimen lots in USNM recorded by Rathbun (1930) under *P. herbstii* (catalog numbers only) plus material added since that time.

North Carolina: 191155. 1M, 1F; sea wall near Pivers I., Beaufort, Carteret Co.; J. B. Sullivan and W. Kirby-Smith, 22 March 1978.—191156. 1M; Pivers I., Beaufort; J. B. Sullivan, 8 April 1978.—191157. 1M; Pivers I., Beaufort; J. B. Sullivan, 10 May 1978.—191158. 2M; Pivers I., Beaufort; J. B. Sullivan, 10 July 1978.—75243. 2M, 1F; Bogue Sound, Morehead City; Shoemaker and Bell, 3 September 1934.

South Carolina: 15784, 57011.

Georgia: 89063. 1M; Georgia coast; State Game and Fish Comm. 1948?

Florida: 15417, 15421, 15742, 15768, 39122, 42849, 56379, 57846, 59840.—72840. 2M; Lemon Bay, Englewood; S. Springer, January 1936.—72841. 2F; Lemon Bay, Englewood; S. Springer.—72851. 8M, 1F; Lemon Bay, Englewood; S. Springer.—78379. 2M, 2F (ovig.); near Sarasota; Bass Biol. Lab., 17 May 1938.—173113. 2M; Sope Hoppy, FSU Marine Lab.; B. Hazlett, June 1978.—81368. 1M; Pensacola Beach; R. O. Christianson, 16 October 1939.

Mississippi: 87387. 1M; Gulf Coast Research Lab. [?]; J. F. Walker, summer 1948.

Louisiana: 2256, 56839.—64150. 1M; Grand Pass, Lake Borgne; S. Springer.—75647. 1M, 2F (1 ovig.); E and Grand Terre Is.; in heavy mangrove roots; E. H. Behre.

Diagnosis.—Carapace noticeably arched dorsally, with few if any transverse lines of granules, coarse granules on ocular and hepatic regions and along anterolateral slopes, length 59.3-75.5% width, \bar{x} 70.1. Coalesced first and second anterolateral teeth of carapace usually separated by shallow rounded notch, second tooth broader than and sometimes more prominent than first; remaining teeth usually rounded, not outstanding (but variable in this respect), fifth tooth shorter than fourth; arc drawn along tips of first 4 teeth converging laterally with arc drawn along bases of notches between teeth. Chelipeds microscopically granular over most of surface (often in obsolescent rugose pattern) but bearing distinctly coarser, closely crowded granules along anterior edge of carpus and on upper and outer surface of palm; distinct reticulate pattern of color on outer surface of palm usually continued over its lower half (may be faded but evident after long preservation). Major chela with teeth on fixed finger varied in size, one or more distal to level of basal tooth on dactyl enlarged, with cusps raised above straight line drawn between angle at juncture of finger with anterior margin of palm and tip of finger (= length of fixed finger); cusps of teeth on fixed finger rather well separated, not broad, seldom worn, their external faces not flared or bowed outward but aligned along axis of finger.

Measurements in mm.—A set of measurements for length and width of the carapace of this species is summarized in Tables 1 and 2 and graphically represented in Figure 9.

Color.—Male somewhat slate blue to dull maroon dorsally, lighter on cardiac and intestinal regions, buff or tannish lines more or less separating regions. Chelipeds with same color as carapace, densest dorsally but breaking into a reticulate pattern of color made up of discrete dark spots on light background on both inner and outer sides of palm, carpus, and merus, continued nearly to ventral side but spots becoming progressively more widely spaced and lighter ventrally; palm with inner and outer central longitudinal stripe relatively colorless, thin proximally but widening distally, a much thinner light line below this on outer side; fingers brown, color continued slightly but variably on palm, tips light. Walking legs tinted dorsally somewhat as carapace but lighter distally (becoming somewhat olive). Eye-stalks with alternate longitudinal stripes of broad gray and narrow dull olive, cornea dark. Antennules with dark and lighter slate blue banding, tipped by off-white brush. External maxillipeds with patches of darker and lighter slate blue banded by off-white on merus; ischium with internal burgundy spot near base variable in size. Tips of raised parts on lower side of legs and venter off-white.

The reticulate pattern on the outer surface of the palm may fade but basically remains after long preservation in 70% ethanol. (From specimens at Beaufort, N.C., and preserved in the USNM.)

Type-locality.—The type-locality is hereby restricted to Egmont Key (mouth of Tampa Bay), Fla.

Known range.—The known geographic range of this species, represented by material listed above, is marsh edge, shallow intertidal, and subtidal waters of the Carolinian Province from environs of Beaufort, N.C., to Georgia (and perhaps northeastern Florida), and from Sarasota County, Fla. to Louisiana. D. L. Felder⁴ has records of the species from Texas and northeastern Mexico. Reames and Williams (1983) and Sullivan et al. (1983) show that the species is mainly associated with marshlands of the Carolinian Province.

Remarks.—Smith (1869a) included syntypic ma-

⁴Darryl L. Felder, Associate Professor, Department of Biology, University of Southwestern Louisiana, Lafayette, LA 70504, pers. commun. 1981-82.

terial from Aspinwall (= Colón, Panama) in the type-series of his variety, but it is evident, after examination of that type-series in the YPM, that the Panama material is *Panopeus lacustris*. The Egmont Key specimen is a well-preserved immature female, cl 8.7 mm, cw 13.0 mm, which lacks one leg, the first walking leg on the left side.

The general shape of the carapace fits that for *P. obesus* at this stage of development: smooth dorsally, branchial areas somewhat inflated, arched antero-posteriorly; anterolateral teeth rounded at apices, first two being almost completely coalesced; front not prominent.

The chelipeds are representative of a large series of the specimens examined, though not fully developed at this size. The right major chela has a well-developed tooth row on the fixed finger with proximal molar area prominent, not broadened, and with cusps somewhat sectorial in nature, forming a row in line with the trend of the finger. The minor chela has a somewhat damaged fixed finger, the distal one-fourth having apparently been broken off but healed; otherwise it is characteristic.

There is no indication of color or color pattern, except for brownish gray darkening of the fingers on both chelae, with tips of fingers and cusps of teeth lighter, and a definite faded internal basal oval spot on the ischium of the third maxillipeds.

Other remarks are given in the general discussion below.

Panopeus simpsoni Rathbun, new rank

Figure 8

Eupanopeus herbstii.—Rathbun 1900b:138 (key, part).

Panopeus herbstii forma simpsoni Rathbun 1930:337, pl. 157, figs. 1-2.—Martin et al. 1984:537-602, figs. 10b, 11b, 13b ii, 14, 18, 23b ii, 24, 25, 33b ii, 34, 35, 36, 46, 47.

Panopeus herbstii.—Rathbun 1930:340-342 (part, *forma typica* from Gulf of Mexico and Bahamas).—Behre 1950:24 (list).—Williams 1965:196 (part).—1984:412 (part).—Felder 1973:69 (part, key).—Powers 1977:102 (part, notes).

Panopeus herbstii forma typica.—Behre 1950:24 (list).

Panopeus herbstii forma Stimpson.—Pounds 1961:4 (list), pl. IX, fig. 2.—Leary 1964 and 1967:44 (list, unnumbered plate and fig., p. 39.

Panopeus herbstii forma simpsoni.—Heard 1982:50, fig. 55a-c.

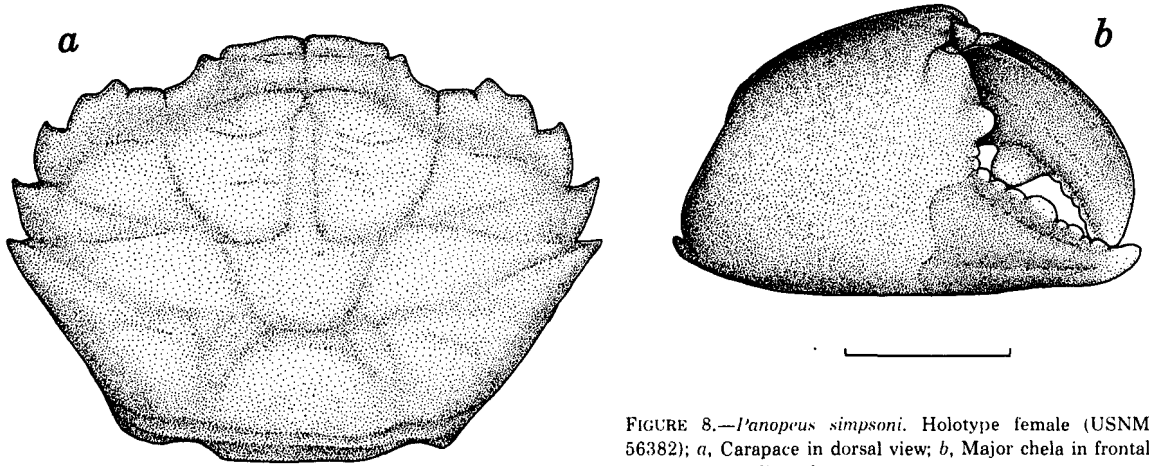


FIGURE 8.—*Panopeus simpsoni*. Holotype female (USNM 56382); a, Carapace in dorsal view; b, Major chela in frontal view; 10 mm indicated.

Material examined.—Specimen lots in USNM recorded by Rathbun (1930) under *P. herbstii* (catalog numbers only) plus material added since that time.

Florida: 6433, 6985, 15413, 15637, 56360, 56382, 56841, 60806, 60919, 61377, 62545.—75648. 1M; Key West; U.S. Bur. Fish.—15415. 1M; South Florida; D. Stearns.—110390. 1M; Tampa Bay; Bur. Com. Fish., 31 July 1962.—65615. 1M; near Wakulla, among oysters; B. C. Marshall, July 1931.—75650. 1M, 1F (ovig.); Apalachicola; A. S. Pearse, 16 June 1935.—75652. 5M, 6 juv.; St. Vincents Bar, Apalachicola; A. S. Pearse, 25 September 1935.—75651. 1F parasitized with *Sacculina*; Hagen's Flats, Apalachicola; A. S. Pearse, 9 January 1936.—89451. 1F (ovig.); Picalyne Bar, Apalachicola; A. S. Pearse, Stn. 319, 9 August 1935.—99860. 1M, 2F; Intracoastal Waterway, 3.5 mi E Interarity Point, Pensacola; F. Berry & A. Mead, 15 August 1953.

Louisiana: 64149. 1M; Grand Pass, Lake Borgne; S. Springer.—98142. 1F; Lake Pontchartrain, 0.5 mi off Bayou St. John, 33 ft; R. M. Darnell, 3 November 1954.—75627. 1M; Grand Isle, Landry's Oyster Reef; E. H. Behre, 12 June 1936.—81369. 9M, 14F (2 ovig.); Bay des Ilettes; E. H. Behre, 13 July 1939.

Texas: 17101, 20639, 33029, 33030.—191174. 2M, 1F; Lower Lavaca Bay, Sand Point Reef; B. D. King III, 4 October 1966.—63275. 1M; Corpus Christi; M. E. Quisenberry.

Locality unknown: 60805. 1M; *Fish Hawk*, U.S. Bur. Fish. tin tag #174.

Types.—The following are designated and labelled as types deposited in the crustacean collection of the USNM: 56382, holotype female, cl 35.9 mm, cw 35.2 mm, Saint George's Sound, Apalachicola, Fla.; E.

Danglade, *Fish Hawk* col., 16 July 1915; 191159, 6M, 1F, transferred from above lot and considered as paratypes.

Diagnosis.—Carapace relatively narrower than that of most other species in complex, length 68.2-77.1% width, \bar{x} 73.5. Coalesced first and second anterolateral teeth separated by deep rounded notch, adjacent slopes of each tooth nearly equal and tip of second nearly as advanced as that of first; fourth tooth not curved forward as much as third; fifth much smaller than fourth, usually projecting straight anterolaterally but sometimes slightly swept forward or hooked anteriorly. Chelipeds superficially smooth but actually finely granulate on upper surface of carpus and palm; lower outer surface of palm light colored (buff or yellowish); major chela with cusps of teeth on fixed finger usually either reaching or falling below straight line drawn between angle at juncture of finger with anterior margin of palm and tip of finger (= length of fixed finger); anterior margin of palm with distance between crest at base of dactyl and tip of condylar tooth lateral to base of dactyl 0.80 or more times length of fixed finger.

Measurements in mm.—A set of measurements for length and width of the carapace of this species is summarized in Tables 1 and 2 and graphically represented in Figure 9.

Color.—Carapace light olive to yellowish or variegated grayish brown on lighter background. Chelipeds with darker of these colors on carpus and palm dorsally, often in mottled pattern (but not reticulated pattern of dots) extending about halfway down inner and outer surface; lower half of palm

yellowish to cream or off-white; fingers brown with white on tips and edges of teeth, shades of light brown to tan on inner surface of fingers. Walking legs variegated as carapace. (From color slide by D. L. Felder; see also Reames and Williams 1983.) Third maxillipeds of males with red spot near base of inner surface of ischium, females lacking spot (Heard 1982).

Known range.—The known geographic range of this species, represented by the material listed above, is shallow intertidal and subtidal waters of the northern Gulf of Mexico: Key West, Fla. (1 doubtful lot); Lee County, Fla., to Corpus Christi, Tex.

Remarks.—See general discussion below.

Key to species of *Panopeus* in the “*herbstii* complex.”

Characters of major chelae refer to original or fully regenerated state.

- 1a. Major chela with cusps of teeth on fixed finger not reaching above imaginary straight line drawn between tip and angle at juncture of finger with anterior margin of palm (= length fixed finger) 2
- 1b. Major chela with cusps of teeth near midlength of fixed finger reaching above an imaginary straight line drawn between tip and angle at juncture of finger with anterior margin of palm (= length fixed finger) 3
- 2a. Coalesced anterolateral teeth 1-2 separated by shallow rounded notch, 2 broader than but not so prominent as 1; 4 curved forward as much as 3; 5 much smaller than 4, acute and hooked forward; palm with distance between crest at base of dactyl and tip of cusp lateral to base of dactyl 0.7 or less length of fixed finger *P. herbstii*
- 2b. Coalesced anterolateral teeth 1-2 separated by deep rounded notch, adjacent slopes of each about equal, 2 nearly as prominent as 1; 4 not curved forward as much as 3; 5 much smaller than 4, usually projecting straight anterolaterally, sometimes slightly hooked; distance between crest of palm and tip of cusp lateral to base of dactyl 0.8 or more length of fixed finger *P. simpsoni*
- 3a. Major chela with cusps of teeth in “molar area” of fixed finger very broad, often coalesced and worn, their external faces often flared or bowed outward *P. lacustris*

- 3b. Major chela with cusps of teeth in “molar area” of fixed finger somewhat enlarged but separated from each other, in line with axis of finger, not bowed outward 4
- 4a. Anterolateral teeth 3-5 definitely swept forward, acute, anterior margins noticeably concave (especially 3-4) *P. meridionalis*
- 4b. Anterolateral teeth 3-4 curved but not noticeably swept forward, anterior margin of at least 3 rectangular and often rounded 5
- 5a. Anterolateral teeth more or less prominent, arc drawn along tips of first 4 teeth diverging laterally from arc drawn along bases of notches between teeth *P. austrobesus*
- 5b. Anterolateral teeth usually rounded, not prominent, arc drawn along tips of first 4 teeth converging laterally with arc drawn along bases of notches between teeth *P. obesus*

DISCUSSION

The *Panopeus herbstii*, s.l., complex of mud crabs occurring in intertidal and shallow littoral regions of the western Atlantic, especially in estuaries and lagoons, is a discouragingly close-knit group of species with few clear-cut characters. Before the diagnoses offered above were developed, the extent of the differences was unknown (but indicated by several authors), although ground work for making such determinations was laid by finding evidence for specific differences in morphometry and ecology between local populations of *P. obesus* and *P. simpsoni* in the northern Gulf of Mexico (Reames and Williams 1983) and comparably strong evidence for specific differences in hemocyanins and ecology among *P. herbstii*, s.s., *P. lacustris*, *P. obesus*, and *P. simpsoni* in the southeastern United States (Sullivan et al. 1983). The question then was: Were these differences paralleled by morphological evidence that applied to the whole complex throughout the geographic range? Answer was sought by reevaluation of a large series of specimens, including statistical analysis of certain measurements and study of the first male pleopods at high magnification.

The first pair of pleopods in males of many brachyurans exhibit characters that are useful in distinguishing species, but study of these structures in this series by light microscopy and scanning electron microscopy shows no consistent differences.

Carapace length and width were recorded for *P.*

herbstii, s.s., *P. simpsoni*, *P. obesus*, and *P. lacustris* from throughout their ranges as determined from the series in the USNM. Characters of the chelae were noted as these measurements were made, and it was seen that the specimens assorted into two apparent groups: 1) Those with major chelae in which cusps on the fixed finger almost always reached or fell below (rarely exceeded) a straight line drawn between its tip and the angle formed by its base and the anterior margin of the palm—the *herbstii-simpsoni* group, and 2) those with major chelae in which some cusps on the fixed finger were raised above or exceeded such a line (if the chela was not regenerating or otherwise altered)—the *lacustris-austrobesus-obeus* group.

Members of the first group have a carapace which is relatively narrower than those of the second group (Tables 1-2, Fig. 9), *P. simpsoni* being the narrowest of all, (a point made by Rathbun 1930), the regression line describing this width-length relationship cutting across analogous lines for the other species. Moreover, the major chela of *P. simpsoni* is relatively larger than that of *P. herbstii*, an observation that is difficult to quantify but one that can be expressed by the relationship of the height of the anterior margin of the palm (i.e., region above articular condyle of dactyl) to the length of the fixed finger. This relationship is greater in *P. simpsoni* (≥ 0.80) than in *P. herbstii* (≤ 0.70). In addition, both of these species have similarly smooth surface granulation; variably mottled dorsal coloration; and third maxillipeds with a basal red spot on the internal surface of the ischium in males, in about 50% of female *P. herbstii* (see

Williams 1965), but never in females of *P. simpsoni* (see Heard 1982).

Rathbun (1930) conceived the center of distribution for *P. simpsoni* to be the northern Gulf of Mexico, but she considered some specimens from South Carolina to belong to this group as well and found specimens of *P. herbstii* from Virginia to vary toward *P. simpsoni*. *Panopeus herbstii* exhibits considerable variation in form of the anterolateral teeth, some specimens from South Carolina resembling in acuteness those of *P. simpsoni*, as do other specimens from as far north as New Jersey. Among such variants are females with internal red spots on the ischium of the third maxillipeds. On the whole, the Atlantic *P. herbstii* is morphologically distinct from the Gulf of Mexico *P. simpsoni*, as confirmed by electrophoretic patterns of the respective hemocyanins (Sullivan et al. 1983).

Members of the second group are relatively larger and more robust than those of the first group, more coarsely granular on carapace and chelipeds, and they share curious veined or reticulate patterns of coloration on the outer surface of the chelae which often extend from the upper to lower margin of the palms. This pattern is rarely seen in members of group 1. Both males and females have a proximal red spot on the inner surface of the ischium of the third maxilliped.

Teeth of the fixed finger of the major chela (except for certain regenerated examples) are developed into a conspicuous raised "molar area" in the proximal and middle parts of the prehensile edge. This development is extreme in *P. lacustris* in which teeth of the molar area are impacted, often worn flat at their crowns, and broadened such that their lateral faces and that of the adjacent finger are bowed or swollen laterally. This development is seen in either right- or left-handed individuals, but some, evidently with chelae in an intermediate stage of development or regeneration, do not exhibit the extreme molar development. *Panopeus obesus* has the molar area developed but its teeth are not impacted or conspicuously broadened and are arranged in line with the axis of the finger; the fingers are relatively longer than those of *P. lacustris*. A counterpart to the tooth pattern of *P. obesus* is found in *P. austrobesus*.

The carapace of *P. obesus* tends to be tumid, with rounded anterolateral teeth; *P. lacustris* has a less tumid carapace, with regions often well developed and angular anterolateral teeth; the carapace of *P. austrobesus* resembles the latter, but is somewhat less strongly developed. Rathbun (1930) tacitly recognized this southern Brazilian population in that

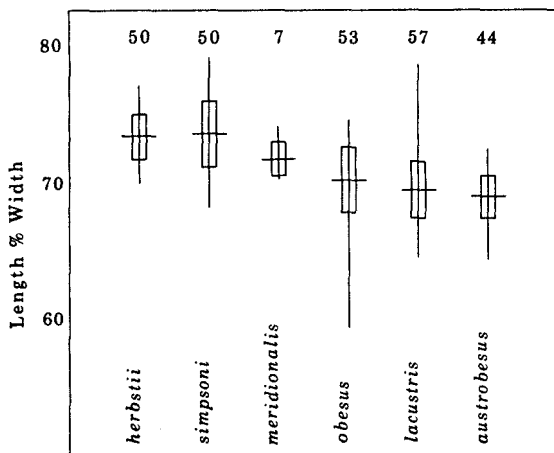


FIGURE 9.—Proportional values and basic statistics for length percent width for samples of six species of *Panopeus* from the western Atlantic. Top row of numbers = *N* in samples, vertical bars = range, horizontal bars = mean, open rectangles = SD.

she placed most of those specimens which she examined in or near form *obesa*.

A sixth species, represented by a very small sample, is intermediate between the two groups discussed above. Its superficial resemblance to *P. simpsoni* in narrowness of carapace, surface granulation, and lack of a basal red spot on the inner surface of the ischium of the third maxilliped in females is offset by prominence of the molar area aligned with the axis of the fixed finger of the major chela.

The species thus are separable on the basis of carapace width-length relationships, with considerable overlap (Table 1, Fig. 9), which are reinforced by a second character, the shape and dentition of the fixed finger of the major chela. The somewhat obscured width-length relationships are presented as linear regressions for samples of five of the species in Table 2. These were tested with the ANCOVA procedure, but sample size for the sixth, *P. meridionalis*, was too small to allow comparable treatment. At $P = 0.05$, there is a significant difference in linear regression of samples of the groups (species) ($F = 34.4647^*$ with 4, 252 df). The hypothesis that the slopes for this regression are equal is rejected ($F = 24.6288^*$ with 4, 244 df) as is the hypothesis that the intercepts are equal ($F = 31.5588^*$ with 4, 244 df). The Newman-Keuls MRT procedure is able to separate these five species into only four significantly different but overlapping groups. The test thus has limited utility for discrimination, merely restating what was known from visual inspection, and emphasizing the fact that other characters must be used in combination with carapace dimensions in making species determinations.

The ranges of these species fit known zoogeographic distribution patterns for many littoral decapod crustaceans (Perez Farfante 1969; Williams 1965). The tropical species, *P. lacustris*, is widespread from Bermuda and southern Florida through the Caribbean Sea to the region of Cabo Frio, Brazil, and flanked by apparent cognates to the north and south. *Panopeus herbstii*, s.s., is associated with oyster beds along the Atlantic coast of the United States from Boston Harbor to southeastern Florida; the closely related *P. simpsoni* occupies the same habitat in the Gulf of Mexico, and a similar species in Uruguay. *P. meridionalis*, may occupy a comparable niche. *Panopeus obesus*, associated mainly with salt marshes, is distributed in the Carolinian Province from Beaufort, N.C., to northeastern Florida, and from western Florida to northeastern Mexico. *Panopeus austrobesus* seems to be a southern counterpart of the latter, ranging from near Cabo Frio, Brazil, southward, although its precise habitat cannot be determined from the collection data at hand.

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