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THE WESTERN ATLANTIC SNAPPING SHRIMPS RELATED TO *ALPHEUS HETEROCHAELIS* SAY (CRUSTACEA, CARIDEA), WITH THE DESCRIPTION OF A NEW SPECIES

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MARTIN LINDSEY CHRISTOFFERSEN*

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ABSTRACT

Four closely related species of the *Edwardsi* group of *Alpheus*, living exclusively within estuarine environments, are recognized in the Western Atlantic region. *A. heterochaelis* Say was collected in North Carolina, Pará and Paraíba, not having been found in southern Brazil. *A. pontederiae* Rochebrune, previously known only from West Africa, is recorded along the Brazilian coast between Pará and Paraná. *A. estuariensis*, sp. n., is common from Florida to Paraná, while *A. chacei* Carvacho, with which *A. maxilliplanus* Christoffersen is synonymized, is known from Guadeloupe to São Paulo. A key for the recognition of these species, notes on their ecological distribution and remarks on their relationships with other species of *Alpheus* are provided.

INTRODUCTION

Alpheus heterochaelis Say, 1818, was the first species of the genus to be recognized in the Western Atlantic. Descriptions given in the literature are based mainly on specimens from the southeastern United States (Say, 1818; Brooks & Herrick, 1892; Hay & Shore, 1918; Verrill, 1922; Williams, 1965) but this name has been widely used for snapping shrimps throughout the Western Atlantic warm-water region. Holthuis (1956) was the first to note slight morphological differences in Brazilian specimens identified by him as *A. heterochaelis*. Chace (1972) pointed out some misidentifications of West Indian and Brazilian specimens, questioning the occurrence of *A. heterochaelis* to the south of Suriname.

As *A. heterochaelis* has been the most commonly cited species in Brazil (e.g., Smith, 1871; Rathbun, 1900b; Moreira, 1901; Luederwaldt, 1919, 1929; Oliveira, 1940, 1948, 1958; Holthuis, 1956; Gerlach, 1958; Coelho, 1965, 1966, 1967a, 1967b, 1971; Coelho, Koenig & Ramos, 1970; Ramos 1971; Coelho & Ramos, 1972; Corrêa, 1972; Ramos-Porto, Ferreira-Correia & Souza, 1978), I began to reexamine some of the previous identifications under this name and to search for this species along the Brazilian coast.

* Departamento de Sistemática e Ecologia and Núcleo de Estudos e Pesquisas dos Recursos do Mar, Universidade Federal da Paraíba, 58.000, João Pessoa, Paraíba, Brazil.

What was previously known as *A. heterochaelis* turned out to be quite an unwieldy complex. Misidentifications with other common species have in fact been so frequent that it has not been clearly realized that *A. heterochaelis* occurs exclusively within estuarine environments. Furthermore, a group of three related species, which have similar color patterns and share all the characters leading to *A. heterochaelis* in Chace's (1972) key to the Western Atlantic species of *Alpheus*, have been discovered within these particular environments. One of these species was recently described from Guadeloupe (Carvacho, 1979) and Brazil (Christoffersen, 1979).

This paper is an account of the four species of *Alpheus* known exclusively from shallow estuarine environments in the Western Atlantic region. One of these species occurs in similar environments along tropical West Africa, being the sole representative of this particular group of species known from the Eastern Atlantic region.

MATERIAL AND METHODS

Part of the material in the following species accounts was collected during a systematic survey I undertook of the intertidal region of southeastern Brazil, between the States of Espírito Santo and Rio Grande do Sul, in which I was mainly interested in establishing southern range limits for tropical species of alpheoid shrimps. This material, and specimens I collected in Beaufort, North Carolina, are in my collection. Further material has been collected in Paraíba, northeastern Brazil, which is kept in the collections of the Departamento de Biologia, Universidade Federal da Paraíba. The remaining samples are from the following institutions: AMNH, American Museum of Natural History, New York; DML, Duke University Marine Laboratory, North Carolina; IOUSP, Instituto Oceanográfico da Universidade de São Paulo; MCZ, Museum of Comparative Zoology, Harvard University, Massachusetts; MNRJ, Museu Nacional do Rio de Janeiro; MZUSP, Museu de Zoologia da Universidade de São Paulo; USNM, United States National Museum, Washington D.C.

Measurements indicated in the text are expressed in millimeters. The first body measurement indicates combined rostral and carapace lengths, the second combined abdominal and telson lengths, both of which have been taken along the dorsal midline of the body. The first major chela measurement refers to its length, the second to its height and the third to its width. The first minor chela measurement refers to its length and the second to its width. All chelae measurements represent their largest linear dimensions.

Key to the Atlantic species related to *Alpheus heterochaelis* Say

1. Major chela with ventral margin of fixed finger distinctly truncate distally; minor first chela of male not "balaeniceps"-shaped 2
 - Major chela with ventral margin of fixed finger more evenly rounded distally, not distinctly truncate; minor first chela of male "balaeniceps"-shaped 3
2. Antepenultimate segment of third maxilliped broad (less than 3 times longer than wide), flat (without distinct ventral and mesial surfaces) and longer than exopod; color-marked finger tips of major chela relatively fragile, bases distinctly wider than lateral margins; fingers of minor first chela distinctly longer than palm *A. chacei* Carvacho
 - Antepenultimate segment of third maxilliped normal (3.75-4.5 times longer than wide), with distinct ventral and mesial surfaces, and shorter than

- exopod; color-marked finger tips of major chela relatively stout, bases subequal to lengths of lateral margins; fingers of minor first chela about as long as palm *A. estuariensis* sp.n.
3. Fixed finger of major chela with large rectangular ridge on opposable margin of lateral surface, and with two small prominences on mesial surface; lateral branch of uropod with two sharp teeth on posterolateral margin, one on each side of movable spine . . . *A. pontederiae* Rochebrune
- Fixed finger of major chela without large rectangular ridge on opposable margin of lateral surface, and without small prominences on mesial surface; lateral branch of uropod with one sharp tooth on posterolateral margin, lateral to movable spine *A. heterochaelis* Say

SPECIES ACCOUNTS

Alpheus chacei Carvacho, 1979

A. chacei Carvacho, 1979: 455, fig. 4-6 (Holotype: ♂, MNHN 2668. Type locality: Lézarde river, Guadeloupe).

A. maxilliplanus Christoffersen, 1979: 318, fig. 11-13 (Holotype: Ovigerous ♀, MZUSP 4545. Type locality: Balneário de Atalaia, State of Sergipe, Brazil. Other localities: State of Paraíba to State of São Paulo, mud within estuaries, 0.3 to 0.7-5m).

Material. Brasil, *Paraíba*, Rio Paraíba do Norte estuary: 1 spec. M.C.Q. Farias coll. Jan. 24, 1979; 1 spec. from Cabedelo. R. Rosas coll. April 27, 1978; 23 spec. from near Cabedelo port, uncovered from soft mud near low-water line by fishing net, M.L. Christoffersen, M.C. Araújo & J.M. Peixoto coll. Febr. 15, 1980; 3 spec. from Jardim Manguinhos, M.L. Christoffersen coll. Febr. 2, 1980; 2 spec. from Ilha da Restinga, M.C.Q. Farias coll. Jan. 24, 1979; 1 spec. from in front of pier of Praia do Jacaré, 5 m, M.L. Christoffersen, R. Sassi & A.K. Nishida coll. June 13, 1980; 4 spec. from near Rio Mandacaru, M.L. Christoffersen & R. Sassi coll. July 3, 1980.

Remarks. As the type material of *A. maxilliplanus* Christoffersen (1979) agrees in all important details with the descriptions and figures of *A. chacei* Carvacho (1979), including the setae on the telson and uropods, more fully illustrated by the latter author, while the small ventrolateral spine on the basal segment of the antenna, not mentioned by that author, is fragile and occasionally damaged in Brazilian material, I am convinced that they represent the same species, and have considered both names synonymous. The description of *A. chacei*, published on June 30, 1979, has date priority over the description of *A. maxilliplanus*, published in the last trimester of 1979.

Habitat. Restricted to estuarine environments, the species is known with certainty only from shallow burrows in soft mud, from low-water line of spring tides to 5 m deep.

Geographical distribution. Guadeloupe; Paraíba to São Paulo.

Alpheus estuariensis sp.n.

(Fig. 1, 2)

Alpheus heterochaelis. Evermann, 1892 (not Say, 1818): 90 (Galveston Bay, Texas, pier). — p.p. Rathbun, 1900b: 152 (Mamanguape, Paraíba, stone reef). — p.p. Schmitt, 1924: 65 (Spanish Water, Curaçao).

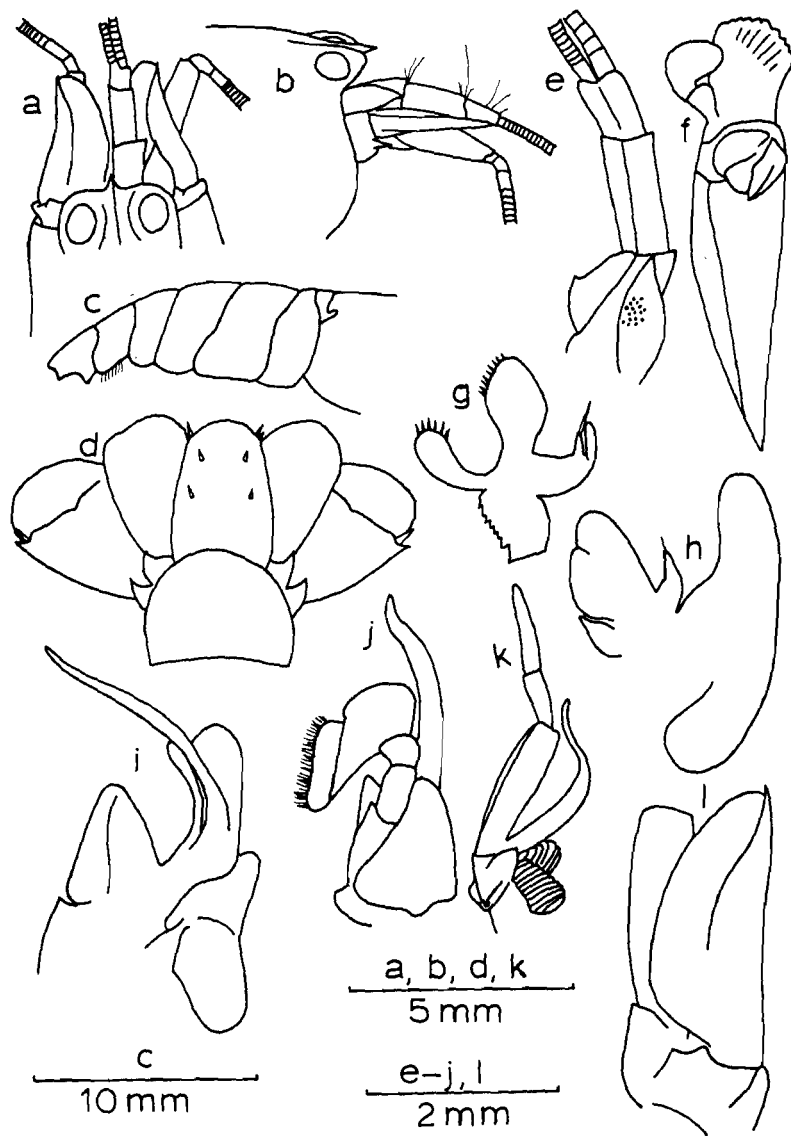


Fig. 1. — *Alpheus estuariensis* sp. n., paratype, ovigerous female from Ilha da Casca, São Paulo: a, anterior region, dorsal view; b, same, lateral view; c, abdomen, lateral view; d, telson and uropods, dorsal view; e, antennule, ventrolateral view; f, mandible; g, first maxilla; h, second maxilla; i, first maxilliped; j, second maxilliped; k, third maxilliped. Paratype, ovigerous female from Gamelheira, Pernambuco: l, antenna, dorsal view.

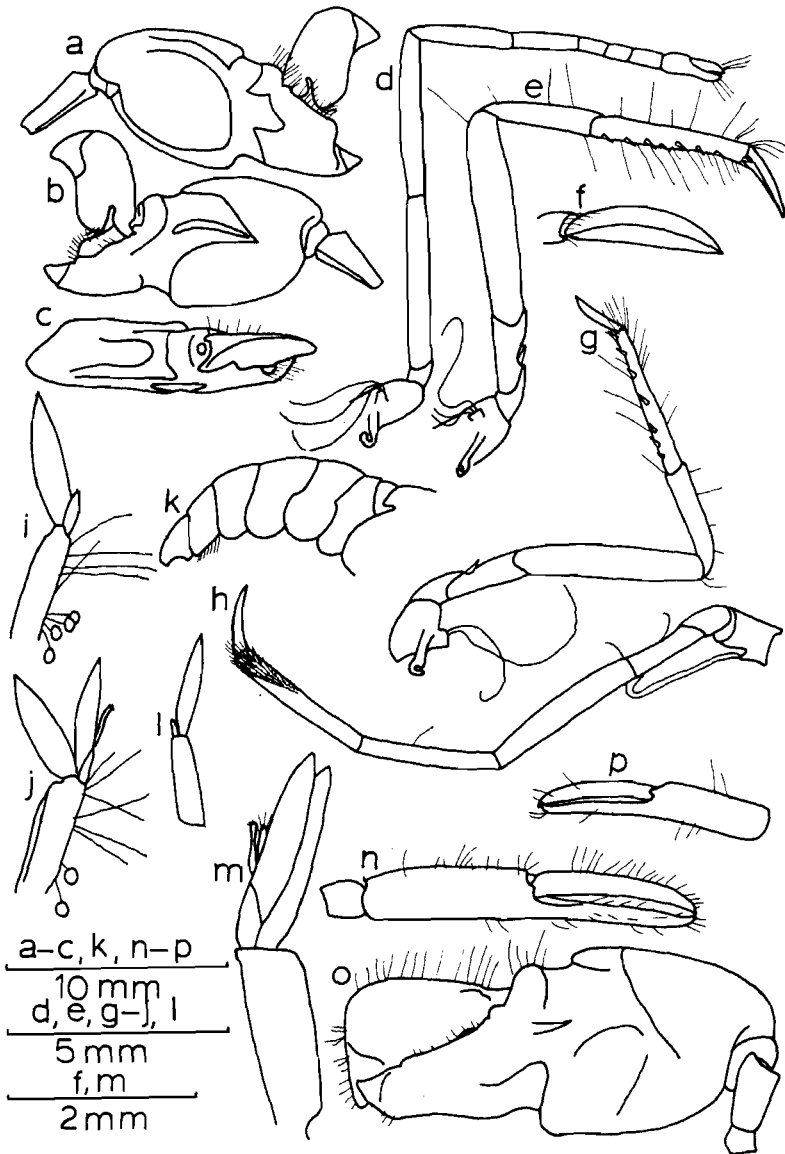


Fig. 2. — *Alpheus estuariensis* sp. n., paratype, ovigerous female from Ilha da Casca, São Paulo: a, major cheliped, mesial surface; b, same, lateral surface; c, same, dorsal surface; d, second pereopod; e, third pereopod; f, dactyl of same; g, fourth pereopod; h, fifth pereopod; i, first pleopod; j, second pleopod. Paratype, male from Ilha da Casca, São Paulo; k, abdomen, lateral view; l, first pleopod; m, second pleopod. Holotype, male: n, minor first chela and carpus, lateral surface; o, major cheliped, lateral surface. Paratype, ovigerous female from Rio Potengi, Rio Grande do Norte: p, minor first chela, mesial surface.

Holotype. ♂, MZUSP 4544; Rio Potengi estuary, Natal, State of Rio Grande do Norte, Brazil, in shrimp nurseries, mud, S.L.S. Bueno coll. Jan. 26, 1979.

Paratypes. Brasil, *Rio Grande do Norte*. Natal, Rio Potengi estuary: 1 ♂, 1 ovig. ♀, from shrimp nurseries, mud, S.L.S. Bueno coll. Jan. 26, 1979; 1 ♂, 1 ovig. ♀ (MNRJ 64-64), from Praia do Forte, A. Lemos de Castro coll. Jan. 25, 1964. *Paraíba*. Mataraca, Barra de Camaratuba, 2 samples (10 ♂, 5 ♀, 1 ovig. ♀) (MNRJ 69-64), A. Lemos de Castro coll. Jan. 31, 1964; Mamanguape, stone reef, 1 ovig. ♀ (part of USNM 25800), Branner-Agassiz Expedition, A.W. Greeley coll. June 20-22, 1899. *Pernambuco*. 1 ♂, 2 ovig. ♀ (one with *Probopyrus* sp in branchial chamber) (MNRJ), coll. Jan. 31, 1959; Recife, Gamelheira, 19 spec (11 ovig. ♀) (MNRJ), H. Schubart coll. *Rio de Janeiro*. Ilha Grande-Setetiba, 2 ♂, 1 ♀ (USNM 144014), Dec. 10, 1970. *São Paulo*. Cananéia: 1 ovig. ♀ from Mar de Cubatão, intertidal region, under stones in mud-sand sediment, M.L. Christoffersen coll. Nov. 8, 1976; 3 samples (4 spec.) (IOUSP) from Mar de Cananéia, 0.5-0.8 m, 26.02-28.90°C, 17.30°/00, coll. Dec. 27, 1973, March 13 and April 3, 1975; 1 spec. (IOUSP) from Baía do Trapandé, 0.5 m, 24.10°C, 19.20°/00, coll. Nov. 20, 1973; 1 ♂, 1 ovig. ♀ from Ilha da Casca, intertidal region, between stones and mud, M.L. Christoffersen coll. Nov. 10, 1976. *Paraná*. Antonina: 1 ♂, 1 ovig. ♀ from in front of county market, intertidal region, in mud under stones, M.L. Christoffersen coll. Febr. 26, 1978; 3 ♂, 1 ovig. ♀ from Ponta da Pita, intertidal region, under stones, among mud and shell fragments, M.L. Christoffersen coll. Febr. 26, 1978.

Other material. U.S.A., *Florida*. Duval County, Saint Johns River, San Carlos Creek, near New Berlin, 2 ♂, 3 ♀ (USNM 90597), Lane coll. Aug. 30, 1949; Indian River, 5 spec. (AMNH 250), C.S. Allen coll. *Mississippi*. Ocean Springs, 5 m, 1 ovig. ♀ (USNM 92256), J.F. Walker coll. 1950. *Louisiana*. Lake Pontchartrain, 4.8 km northeast of Irish Bayou, 4 m, 13.5°C, 6.7°/00, 1 ♂ (USNM 98137), R.M. Darnell coll. Feb. 18, 1955; Rigolets of Lake Borgne, 22 m, 14.8°C, 2.4°/00, 1 ♂ (USNM 98138), R.M. Darnell coll. Feb. 5, 1954; East Pearl River, Kelleys Point, 30°11'N-89°34'W, 20.0°C, 0.3°/00, 1 ♂ (USNM 98136). R.M. Darnell coll. March 4, 1955. *Texas*. Galveston Bay, pier. 2 ♂ (USNM 63546), U.S. Fish. Comm., B.N. Evermann coll. Nov. 5-15, 1891. *Cuba*. Varadero, Laguna de Paso Malo, 1 ♂, 2 ovig. ♀ (USNM 96455), J.F. Millers coll. Dec. 23, 1953. *Dominican Republic*. Santo Domingo, southern and inner portion of El Cayo, 1 spec. (AMNH 8664), J.C. Armstrong coll. May 8, 1933. *Trinidad*. Coroni Swamp, mouth of Blue River, 1 ♂, 1 ovig. ♀ (USNM 120487). P.R. Bacon coll. April 8, 1966. *Curacao*. Spanish Water, 4 spec. (USNM 57522), C.J. Van der Horst coll. May 19, 1920. *Brasil*. 2 ♂, 2 ovig. ♀ (MNRJ). *Ceará*. Fortaleza. Barra do Ceará, 10 spec. (MNRJ 62-64), A. Lemos de Castro coll. Jan. 22, 1964. *Paraíba*. Mataraca, Barra de Camaratuba, intertidal region, in soft mud, 3 ♂, 4 ovig. ♀, 5 juveniles, M.L. Christoffersen coll. Nov. 22, 1980; Rio Paraíba do Norte estuary: 35 spec. from Costinha, intertidal region, mud, M.L. Christoffersen coll. May 1, 1981; 3 samples from Ilha da Restinga, M.C.Q. Farias coll. Dec. 9, 1977, March 8, 1978 and M.L. Christoffersen coll. Nov. 26, 1980; 2 samples (12 spec.) from Jardim Manguinhos, intertidal region, in mud among *Rhizophora* roots, M.L. Christoffersen coll. Feb. 15, 1980, and May 3, 1981; 10 spec. from Praia do Jacaré, intertidal region, mud, M.L. Christoffersen coll. May 1, 1981; 20 spec. from Rio Jaguaribe, intertidal region, soft mud to sandy mud, inside and outside of mangrove, M.L. Christoffersen coll. May 6, 1981; 7 spec (4 ovig. ♀) from margins of Rio Paraíba, intertidal region, in mud

under rotten tree trunk, M.L. Christoffersen coll. Nov. 20, 1979; 3 ovig. ♀ from Salina Santa Maria, O. Travassos coll. Jan. 28, 1978; 2 samples (6 spec.) from mouth of Rio Tambiá, intertidal region, sandy-mud flat, M.L. Christoffersen coll. March, 1980 and R. Sassi coll. May 14, 1980.

Description. Rostrum (Fig. 1 *a, b*) sharp, slightly carinate dorsally, reaching one-third to two-thirds of length of visible portion of the basal antennular segment. Ocular hoods produced dorsally, separated from rostrum by distinct depressions, which in the posterior region merge gradually into dorsal surface of carapace. Frontal margin of ocular hoods approximately straight. Anterior margin of carapace almost straight from ocular hood to ventral margin of antennal peduncle. Posterior margin of carapace (Fig. 1 *c, 2 k*) with pronounced cardiac notch.

Abdominal pleurae of five anterior somites (Fig. 1 *c, 2 k*) with rounded, broadly overlapping ventral margins. Sixth abdominal somite produced into narrowly rounded triangular lobe dorsal to insertion of uropod.

Telson (Fig. 1 *d*) sixth-fifths to five-thirds longer than wide at base, about twice as long as wide at distal portion; lateral margins nearly straight; posterior margin convex, with posterolateral spines not reaching as far as apex of telson. Anterior pair of dorsal spines inserted slightly anterior to midlength of telson, posterior pair approximately midway between anterior pair and apex of telson.

Antennular peduncle (Fig. 1 *a, b, e*) with stylocerite broad at base, narrowing abruptly into short spine which reaches distal margin of basal segment. Ventral carina of basal antennular segment rounded or produced medially into an obtuse, curved tooth. Second antennular segment subequal to length of first, about twice as long as third. Thickened portion of dorso-lateral flagellum of antennule equal in length or slightly longer than peduncle, consisting of 16-25 articles; the following 31-39 narrow articles have on the side a vestigial flagellum of 1-3 articles.

Antennal scale (Fig. 1 *a, b, l*) with blade reaching about to end of antennular peduncle; lateral spine slightly longer or not overreaching blade. Antennal peduncle slightly longer than blade; basal segment with sharp ventro-lateral spine below scale, shorter than stylocerite.

Mouth parts as figured (Fig. 1 *f-k*). Third maxilliped reaching to end of antennal peduncle; exopod reaching midlength of penultimate segment of endopod; antepenultimate segment about twice as broad as distal segments, 3.75-4.5 times longer than large, triangular in cross section, mesial surface with about one-third of width of dorsal and ventral surfaces; last segment unarmed, 1.5-2 times longer than penultimate segment.

Branchial formula characteristic of *Alpheus*, a rudimentary pleurobranch being present at base of the third maxilliped.

Major cheliped (Fig. 2 *a-c, o*) with propodocarpal articulation reaching to anterior margin of carapace. Chela compressed, notched dorsally and ventrally, with irregular depressions and longitudinal grooves on both surfaces of palm; lateral surface of fixed finger with opposable margin slightly elevated along margin of socket and distinctly notched distal to socket; ventral margin of fixed finger truncate near apex, which is thus sharply triangular and slightly shorter than the movable finger; extensor margin of movable finger with proximal and distal parts straight and perpendicular to each other. Merus with flexor margins unarmed distally.

Minor first cheliped with propodocarpal articulation reaching distal end of antennal peduncle. Chela (Fig. 2 *n,p*) straight, subcylindrical, without grooves or depressions, fingers about same length as palm; movable finger rounded, similar in both sexes. Merus with flexor margins unarmed distally.

Second pereiopod (Fig. 2*d*) overreaching antennal peduncle by chela and four distal articles, and sometimes up to half of a fifth article. Chela subequal to length of two distal articles of carpus, palm two-thirds to three-fourths length of fingers. Carpal articles decrease in length as follows: $1 > 2 > 5 > 3 \geq 4$. Merus six to seven-tenths as long as carpus, subequal in length to ischium.

Third pereiopod (Fig. 2*e, f*) overreaching antennal peduncle by dactyl and from half to two-thirds of propodus. Dactyl subspatulate, slightly over one-third or slightly under half as long as propodus. Propodus armed with 4-7 spines, as well as one pair of distal spines, along ventral margin. Carpus about seven-tenths as long as propodus and about half as long as merus. Merus five to almost six times longer than wide. Ischium with movable spine near ventral margin.

Fourth pereiopod (Fig. 2*g*) overreaching antennal peduncle by length of dactyl. Dactyl less conspicuously subspatulate than in third pereiopod, two-sixths to two-fifths as long as propodus. Propodus with 4-7 spines, as well as one pair of distal spines, along ventral margin. Carpus seven-tenths as long as propodus and about half as long as merus. Ischium with movable spine near ventral margin.

Fifth pereiopod (Fig. 2*h*) overreaching antennal peduncle by half to all of length of dactyl. Dactyl inconspicuously subspatulate, from slightly less than one-third to almost half the length of propodus. Propodus with 4-5 single spines along ventral margin, and with several transversal rows of short setae in distal third. Carpus subequal to length of propodus, and four-fifths as long as merus. Merus about nine times longer than wide. Ischium unarmed.

First pleopod (Fig. 2*i, l*) with endopod larger in females than in males. Second pleopod (Fig. 2*j, m*) with appendix masculinum subequal to length of appendix internum in males. Eggs rounded in initial stages of development, and elliptical prior to hatching, increasing in diameter from 0.6 by 0.6 to 0.8 by 1.0 mm, respectively.

Uropod (Fig. 1*d*) with short uncolored movable spine on outer branch, flanked laterally by sharp fixed tooth and mesially by rounded lobe, which is continued into an almost straight transversal suture.

Measurements. Largest male (holotype), body 13/24.5, major chela 19/8.5/4.5, minor first chela 14/2.5. Largest ovigerous female, body 13/24.5, major chela 14.5/6/3.5, minor first chela 11.5/2. Smallest ovigerous female, body 7/13, major chela 9.5/4/2.5, minor first chela missing.

Color. Body with irregularly distributed red chromatophores surrounded by blue pigments, so as to form distinct patches. White pigment occurs between the red-blue patches, sometimes forming narrow irregular bands across the anterior portions of the abdominal somites. Diffuse purple pigment may occur on posterior region of telson and uropods. Mesial surface of major chela may have brown, green and blue pigments. Eggs green or orange.

Remarks. *A. estuariensis* sp. n. is morphologically very close to the previous species, *A. chacei*, but the latter differs in the following points: ocular hoods and rostrum less prominent dorsally; third maxilliped with exopod shorter than antepenultimate segment, latter conspicuously enlarged and

flattened; major chela with finger-tips relatively short and fragile and extensor margin of movable finger slightly more arched dorsally; minor first chela with fingers as much as 1.5 times longer than palm; propodus of third to fifth pereopods unarmed, or with fewer and less conspicuous spinules along ventral margin.

Name. Derived from *aestuarium*, L=estuary, referring to the environment characteristic for this species.

Habitat. Restricted to estuarine environments, this species occurs in burrows from relatively firm sand and mud flats, often associated with hard structures like stones, oysters or mangrove roots, to the extremely soft mud characteristic of water run-offs throughout the mangrove ecosystem. It is frequent in the intertidal region, having been collected from relatively high levels within this region down to 22 m deep. Measured water temperatures vary from 13.5 to 28.9°C, salinities from 0.3 to 19.2‰.

The Branner-Agassiz material from Mamanguape most certainly was collected on the inner side of the stone reef, which is flooded by the Mamanguape river.

Geographical distribution. East coast of Florida; from Mississippi to Texas; Cuba; Dominican Republic; Trinidad; Curaçao; from Ceará to Paraná.

***Alpheus pontederiae* Rochebrune, 1883**

(Fig. 3, 4)

Alpheus pontederiae Rochebrune, 1883: 174 (Mouths of Leybar, Thiank and Dakar-Bango Rivers, Senegal, in floating clusters of *Eichhornia natans*). Holthuis, 1951: 85, fig. 17 (Bonny River, opposite Opofo, Niger Delta, Nigeria, 8-15 m, soft grey mud). Longhurst, 1958: 31 (West Africa). Rossignol, 1962: 131 (Djeno, near Pointe Noire, Congo, lagoon). Crosnier & Forest, 1965: 607; 1966: 278, fig. 23 a-j (Conakry, Guinea, in mangrove channel, intertidal region to 30 m).

Alpheus edwardsi. Aurivillius, 1898 (not *Athanas edwardsii* Audouin, 1826): 30 (river near Bibundi, Cameroon, decayed wood in a river).

Alpheus megacheles. Coutière, 1899 (not *Hippolyte megacheles* Norman, 1868): 37.

Alpheus macrocheles. Rathbun, 1900a (not *Hippolyte macrocheles* Hailstone, 1835): 312. Balss, 1916: 20.

Crangon langi Schmitt, 1926: 20, fig. 63 (Holotype: ♂, AMNH 4799a. Type locality: Banana Bay, east of Banana peninsula, Zaire; intertidal zone, brackish water, under stones, pieces of wood and other hard objects, and in tunnels in mangrove swamps).

Alpheus bouvieri. Monod, 1927 (not A. Milne Edwards, 1878): 594 (Souelaba and Kwele-Kwele Island in Malimba Bay, Cameroon, from decomposing wood).

Alpheus langi. Monod, 1928: 252.

Material. East Atlantic, Zaire. Banana, 1 ♂. Holotype (AMNH 4799a) and 2 ♀. Paratypes (AMNH 4799) of *Crangon langi* Schmitt, H. Lang. & C. Chapin coll. July, 1915. Brasil, Pará. 2 samples (2 ovig ♀) (MCZ), Thayer Expedition, A. Agassiz & Bourget coll. 1865. Maranhão. Carutapera, Rio Arapiranga, 2 ♂, 3 ovig. ♀ (MNRJ), C.S. Ferreira & O. Fontoura coll. 1959.

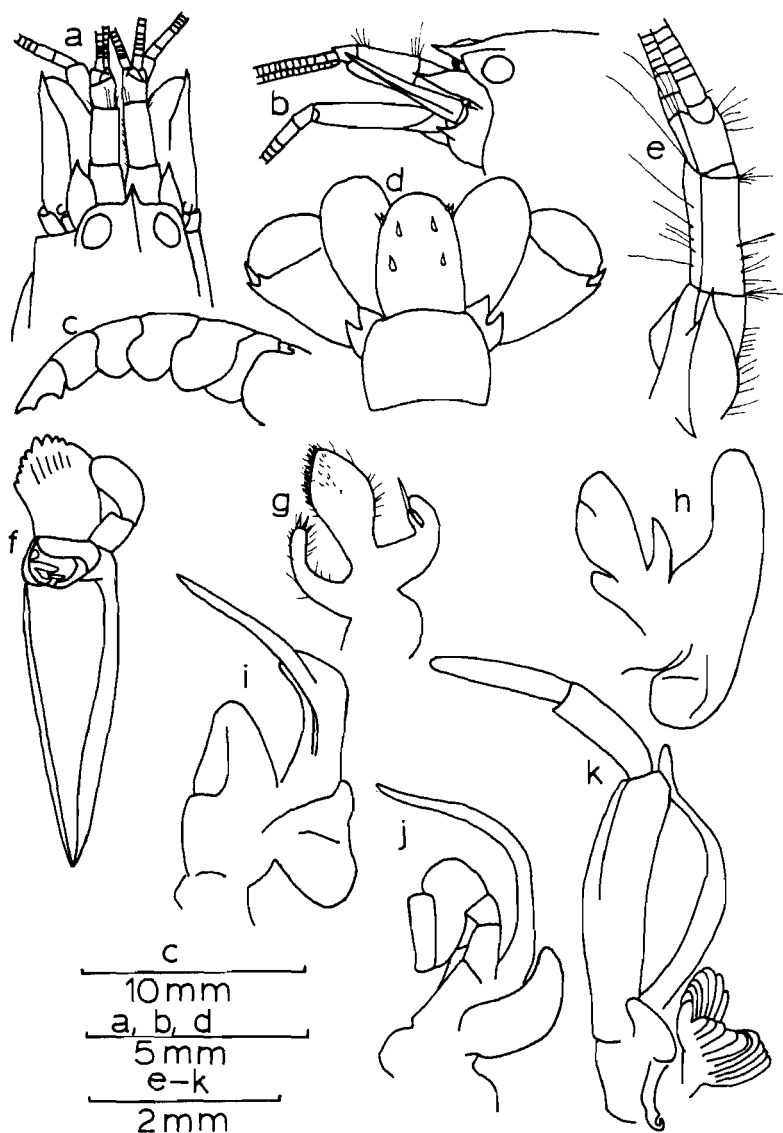


Fig. 3. — *Alpheus pontederiae* Rochebrune, male from Cananéia, São Paulo: a, anterior region, dorsal view; b, same, lateral view; c, abdomen, lateral view; d, telson and uropods, dorsal view; e, antennule, ventrolateral view; f, mandible; g, first maxilla; h, second maxilla; i, first maxilliped; j, second maxilliped; k, third maxilliped.

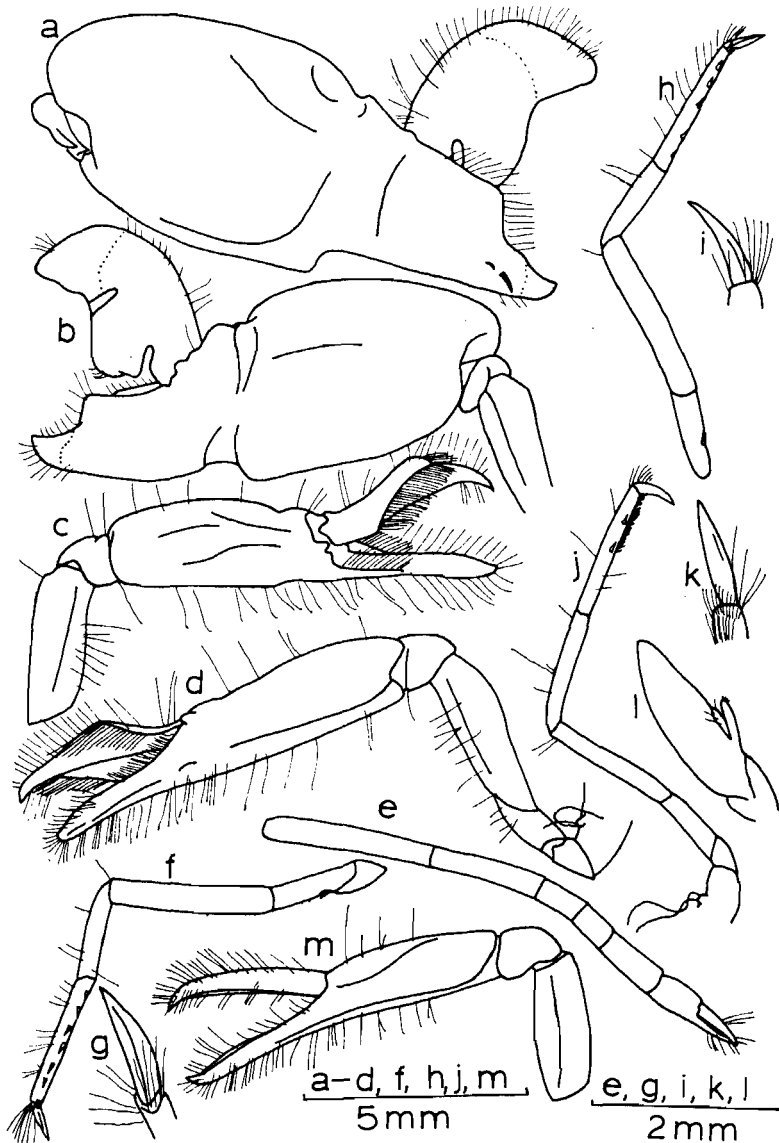


Fig. 4. — *Alpheus pontederiae* Rochebrune, male from Cananéia, São Paulo: a, major chela and carpus, mesial surface; b, major cheliped, lateral surface; c, minor first cheliped, lateral surface; d, same, mesial surface; e, chela and carpus of second pereiopod; f, third pereiopod; g, dactyl of same; h, fourth pereiopod; i, dactyl of same; j, fifth pereiopod; k, dactyl of same; l, endopod of second pleopod. Female from Cananéia, São Paulo: m, minor first cheliped, mesial surface.

São Paulo. Ilha de Santo Amaro, Bertioga channel, intertidal region, in mud under stones, 1 ♀, M.L. Christoffersen coll. Dec. 5, 1976; Cananéia, Mar de Cubatão, intertidal region, in fine sand and mud under stones, 1 ♂, 3 ♀, M.L. Christoffersen coll. Nov. 8, 1976. *Paraná*. Antonina, in front of county market, intertidal region, in mud under stones, 2 ♂, 2 ♀, M.L. Christoffersen coll. Febr. 26, 1978.

Measurements. Largest male, body 14/25, major chela lost, minor first chela 17/4. Major chela of males attains 18/8/4.5. Largest ovigerous female, body 16/30, major chela lost, minor first chela 16/3. Major chela of females attains 16/6/2.5. Smallest ovigerous female, body 11.5/18, both chelae lost.

Color. General body tone greenish, with gray patches and numerous red chromatophores. Traces of blue and purple pigment may occur on distal portions of uropods and ventral margins of abdominal pleurae. Anterior third of major chela brown, finger tips whitish-gray.

Remarks. The species is referred for the first time from the Western Atlantic, the new material being morphologically identical to the examined African type material. *A. pontederiae* belongs to the group of *Alpheus* having a rudimentary pleurobranch at the base of the third maxilliped. It is very similar to *A. heterochaelis* Say, but the latter can be distinguished by the absence of the large rectangular ridge and the small prominences on the finger of the major chela, and by the presence of only one sharp tooth, instead of two, on the posterolateral margin of the outer uropod.

Habitat. The species is known only from estuarine environments, from the intertidal region to 30 m deep. It has been found in decaying wood, floating vegetation or burrows in fine sand and mud, usually associated with hard objects.

Geographical distribution. Pará; Maranhão; São Paulo; Paraná, Eastern Atlantic from Senegal to Zaire.

***Alpheus heterochaelis* Say, 1818**

(Fig. 5-7)

Alpheus heterochaelis Say, 1818: 243 (Type locality: Amelia Island, Nassau County, N. E. Florida, restricted by Holthuis, 1959. Other localities: South Carolina). pp. Brooks & Herrick, 1892: 376, pl. 2 (Beaufort, North Carolina, in beds of oyster shells). Williams, 1965: 66, fig. 54 (Carolinas). Chace, 1972: 67.

Crangon heterochaelis. Hay & Shore, 1918: 386, fig. 8, pl. 26 fig. 6 (Beaufort, North Carolina, burrowed in mud or among oyster shells).

Alpheus or *Crangon heterochaelis*. p.p. Verrill, 1922: 76 (Fort Macon, North Carolina).

Material. U.S.A., *North Carolina*. Beaufort: 2 ovig ♀ (DML 788) from mud flats opposite Gallant Point, Newport River, intertidal region, coll. June 23, 1961; 2 samples (6 spec.) from Radio Island, near bridge to Pivers Island, intertidal region, among oysters and mud, M.L. Christoffersen coll. April 6 and 8, 1978; 1 ♂ from Shackleford jetty, M.L. Christoffersen coll. April 4, 1978: 1 ♂, 1 ♀ from Bird Shoal, on oyster bar, intertidal region, M.L. Christoffersen & A. Kazmi coll. April 6, 1978. *Brasil*. *Pará*. São João de Pirabas, Ilha de Fortaleza, 1 ♂, 2 ♀, 1 juvenile (MNRJ 109-66), A. Lemos de Castro coll. June 14, 1966. *Paraíba*. Rio Paraíba do Norte estuary:

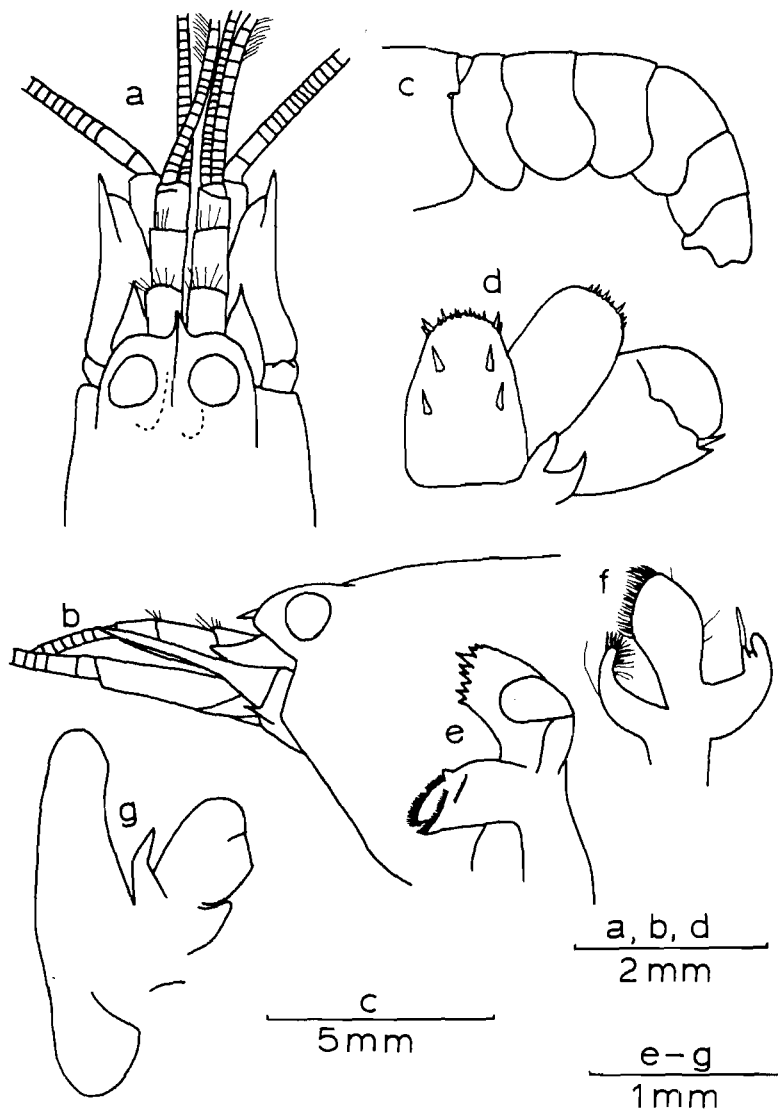


Fig. 5. — *Alpheus heterochaetis* Say, male from Pará: a, anterior region, dorsal view; b, same, lateral view; c, abdomen, lateral view; d, telson and uropod, dorsal view; e, mandible; f, first maxilla; g, second maxilla.

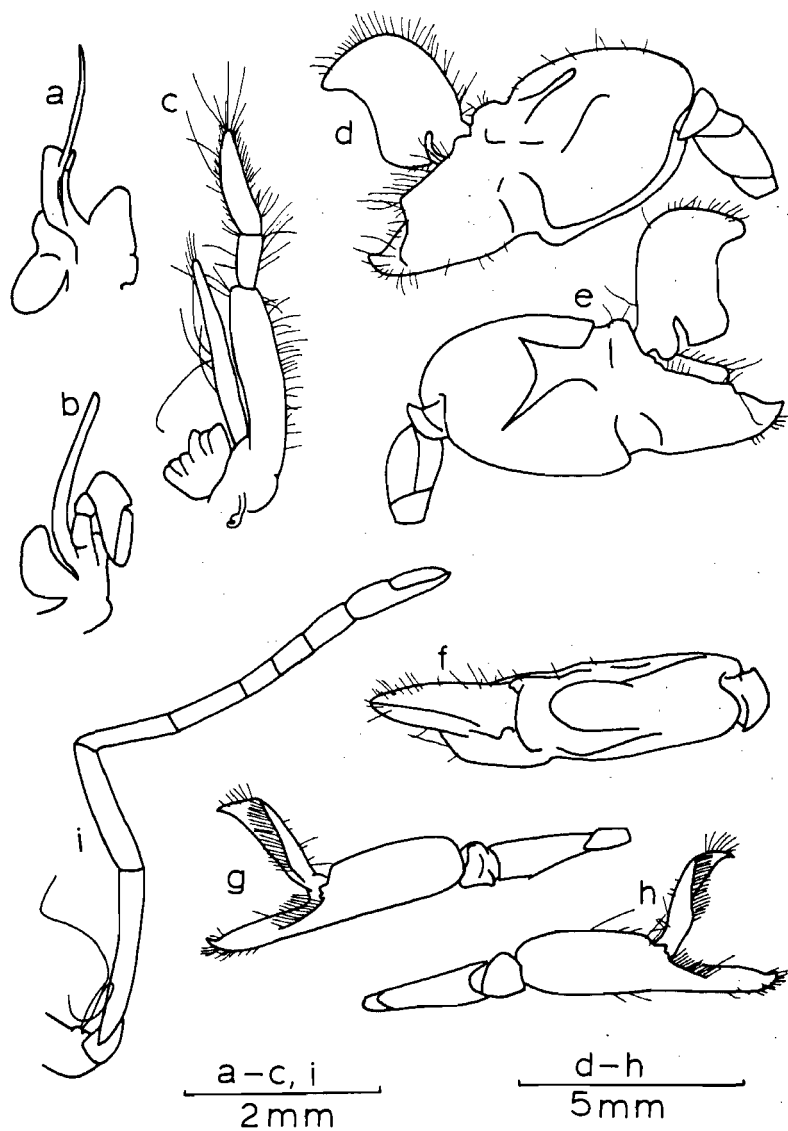


Fig. 6. — *Alpheus heterochaelis* Say, male from Pará; a, first maxilliped; b, second maxilliped; c, third maxilliped; d, major cheliped, mesial surface; e, same, lateral surface; f, same, dorsal surface; g, minor first cheliped, lateral surface; h, same, mesial surface; i, second pereopod.

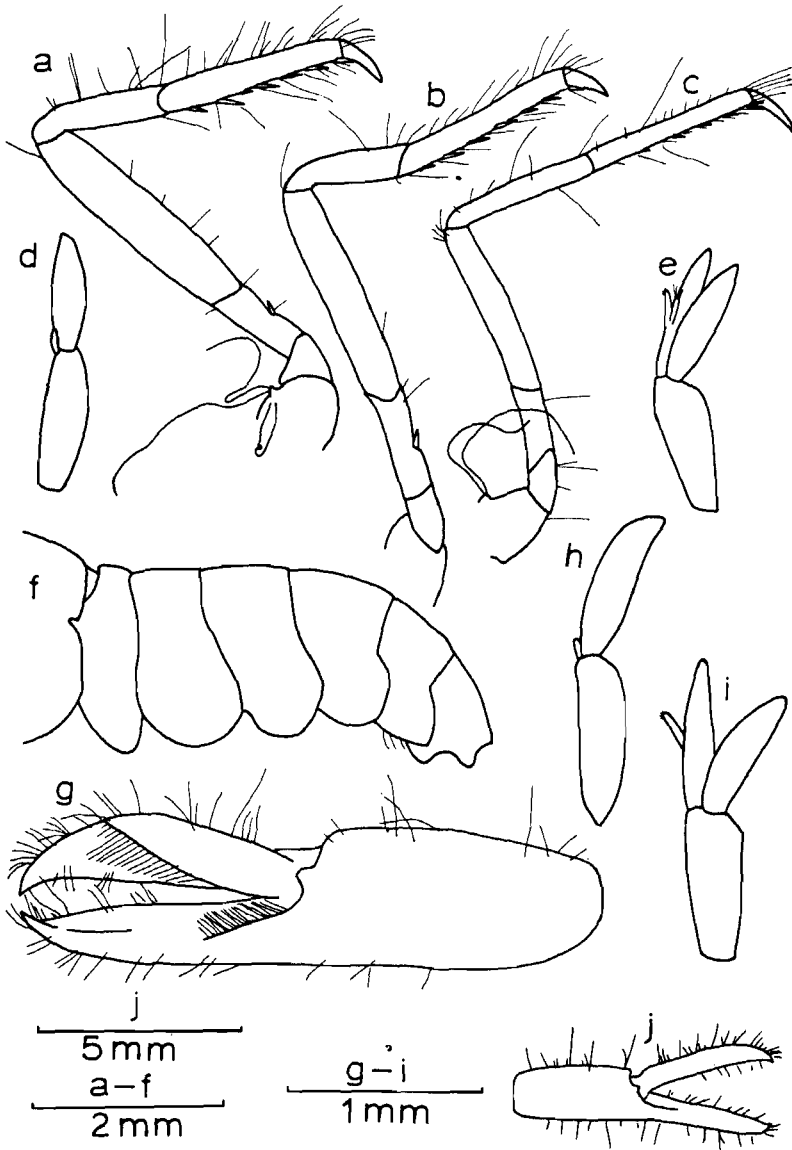


Fig. 7. — *Alpheus heterochaelis* Say, male from Pará: a, third pereopod; b, fourth pereopod; c, fifth pereopod; d, first pleopod; e, second pleopod. Juvenile from Pará: f, abdomen, lateral view; g, minor first chela, lateral surface; h, first pleopod; i, second pleopod. Female from Rio Jaguaribe, Paraíba: j, minor first chela, lateral surface.

2 samples (2 ♂, 1 ovig ♀) from margins of Rio Paraíba, intertidal region, M.L. Christoffersen & R. Sassi coll. Febr. 15 and July 3, 1980; 41 spec. from near Cabedelo port, intertidal region, in sandy mud under stones, M.L. Christoffersen coll. May 5, 1981; 1 ♀ from Rio Paraíba river bed, 9 m, A.D. Assis coll. Febr. 5, 1980; 7 spec. (2 ovig. ♀) from Rio Jaguaribe, intertidal region, firm sandy mud, under stones and oysters, M.L. Christoffersen, coll. May 6, 1981.

Measurements. *Material from North Carolina*: Largest male, body 11.5/21, major chela 15/7/3, minor first chela 11/2. Largest female, body 12.5/22.5, major chela 13.5/7/3, minor first chela 11/2. *Material from Paraíba*: Largest male, body 8.5/17.5, major chela 13.5/6.5/3, minor first chela 10.5/2.5. Largest ovigerous female, body 9/18.5, major chela 12.5/5/2.5, minor first chela 8.5/2. Smallest ovigerous female, body 5.5/10, both chelae lost. *Material from Pará*: Male, body 5.5/10, major chela 8/4/2, minor first chela 6/1.5. Largest female, body 3.5/6, major chela 4/2/1, minor first chela 3/0.75.

Color. Specimens from Paraíba with general body color from light brown to dark blue. Red chromatophores uniformly distributed over body and appendages, some of which, in the lighter animals, and most of which, in the more heavily pigmented specimens, are surrounded by blue pigment, especially over dorsal region of body. Conspicuous blue patches may also occur on telson and uropods. Small irregular white spaces occur between the red and blue patches of body. Major chela brown-green on mesial surface and grey-blue on lateral surface, in lighter colored specimens, while the blue pigment predominates in the more heavily pigmented specimens, including the molar tooth. Finger tips of major chela pinkish. Eggs green or brown.

North Carolina specimens have general body color predominantly green (Brooks & Herrick, 1892; Hay & Shore, 1918; Verrill, 1922; Williams, 1965).

Remarks. The distinguishing characters between this species and *A. pontederiae* Rochebrune have been discussed above.

The juvenile specimen from Pará illustrated in Fig. 7 *f-i*, is slightly atypical in that the minor first chela is "balaeniceps"-shaped (Fig. 7*g*), a male character, but there is no appendix masculinum on the second pleopod (Fig. 7*i*).

Unfortunately Say's type material of *A. heterochaelis* appears to be no longer available. Yet it seems quite reasonable to associate this name with the species known from the Carolinas to northeast Florida, because this is the original site of the type material, because no other species related to *Alpheus heterochaelis* are known north of Florida and because the only detailed descriptions of *A. heterochaelis* are based on specimens from the Carolinas.

Apart from the misidentifications referred by Chace (1972), I have found that specimens assigned to *A. heterochaelis* from Texas (Evermann, 1892) and Curaçao (Schmitt, 1924) belong to *A. estuariensis*, sp.n., while several other published records belong to more than one species. The material listed by Rathbun (1900b) from Pernambuco belongs to *A. bouvieri* A. Milne Edwards, that from Alagoas to *A. nuttingi* (Schmitt), while that from Paraíba belongs to the two previous species and also to *A. armillatus* H. Milne Edwards and *A. estuariensis*, sp.n. The material referred by Smith (1871) from Abrolhos, Bahia, is assignable to *A. armillatus*, while a male specimen recorded by the same author (*l.c.*) from Aspinwall is *A. nuttingi*. Specimens from Bermuda (Kingsley, 1878) refer to *A. armillatus* and *A. bouvieri*, and the lot referred by Verrill (1922) from Key West, Florida, belongs to *A. armillatus*. The material listed by Luederwaldt (1919) from Itanhaém belongs to *A. bouvieri*,

while the specimens from Iguape (*l.c.*) are assignable to *A. armillatus*, *A. bouvieri* and *A. nuttingi*.

The remaining material identified by others as *A. heterochaelis* Say must be reexamined. The specimens recorded by Holthuis (1956) from Cananéia, São Paulo, could be either *A. chacei* Carvacho or *A. estuariensis*, sp.n., while those recorded by the same author (1959) from Suriname could be *A. pontederiae* Rochebrune, as well as *A. heterochaelis* Say. The material from the Gulf of Mexico and Caribbean which I examined before studying the type material of *Alpheus langi* (Schmitt) could likewise be either *A. pontederiae* or *A. heterochaelis*.

Habitat. This is another typical estuarine species, known from the intertidal region to 9 m deep. It occurs in burrows in mud flats or firm sandy-mud river banks, usually associated with oysters or stones.

Geographical distribution. North Carolina to the State of Paraíba, Brazil.

DISCUSSION

The frequent misidentification of specimens as *A. heterochaelis* have obscured the fact that the most common species of *Alpheus* along the rocky, intertidal, non-estuarine environments of the eastern coast of Brazil are *A. armillatus* H. Milne Edwards, *A. bouvieri* A. Milne Edwards and *A. nuttingi* (Schmitt). Within estuaries along this coastline, *A. armillatus* is usually the most common species where rocks and other hard objects predominate in the intertidal region.

Although the local distributions of the species within estuaries are somewhat overlapping, habitat preferences were noted in some cases. *A. heterochaelis* and *A. pontederiae* seem to be always associated with hard objects in the intertidal region, where they may be found under the same stones as *A. armillatus*, although the first two species have not been found together. *A. estuariensis* and *A. chacei* are more common in shallow burrows excavated directly in the sediment, the former predominating in the intertidal region while the latter predominates in the shallow subtidal region. *A. estuariensis*, which possesses the largest amount of unspecialized morphological characters, is the most common species in very soft mud within mangroves and associated sand and mud flats, but is also frequent under hard objects, like oyster shells next to *A. heterochaelis* or under the same stones as *A. pontederiae* or *A. armillatus*. *A. chacei*, on the other hand, which has the largest amount of specialized morphological characters, seems to be restricted to a very narrow zone in the shallow subtidal region, and its broadened third maxillipeds could be some special adaptation to feeding in particularly turbid habitats.

It is possible that biological interactions like competition and predation strongly affect the local distributions of the species of *Alpheus* within estuaries. Evidence for this comes from the overlapping distributions discussed above, and from the fact that, under the same stones at a pier near Cabedelo port, Paraíba, I on one occasion found only *A. armillatus*, whereas 15 month later (May 5, 1981), I collected there both *A. armillatus* and *A. heterochaelis* in about equal numbers. This was even more striking because only on this occasion was I able to confirm the presence of *A. heterochaelis* in Brazil, after searching for this species for several years along the eastern coast of Brazil.

The southern range of *A. heterochaelis* will probably be extended further south along the eastern coast of Brazil, but its absence to the south of the

State of Espírito Santo, where I have collected more thoroughly, may be a significant negative datum. The northern range of *A. pontederiae* may be extended beyond the Brazilian frontier when the Caribbean and Gulf of Mexico material identified as *A. heterochaelis* is reexamined.

In addition to the four Atlantic species from estuarine environments treated in this paper, there are at least another ten Indo-Pacific forms, *A. euprosyne* De Man, *A. mackayi* Banner, *A. macrodactylus* Ortmann, *A. malabaricus dolichodactylus* Ortmann, *A. malabaricus leptopus* De Man, *A. malabaricus malabaricus* (Fabricius), *A. malabaricus songkla* Banner, *A. microrhynchus* De Man, *A. paludicola* Kemp and *A. tirmizae* Kazmi, which seem restricted to brackish-water environments. This group of 14 species shares the following specialized and distinctive morphological characters within the Edwardsi group of *Alpheus*: a) The presence of subspatulate dactyls on third and fourth pereopods (in *A. heterochaelis* these dactyls are not always clearly subspatulate but have a distinct dorsal carina; in *A. microrhynchus* the dactyls are described as conical (Banner & Banner, 1966); b) the presence of a single row of spines along the propodus of the third and fourth pereopods, instead of a series of paired spines (these spines are furthermore often reduced in number, being inconspicuous among long and numerous setae or totally absent). Other distinctive trends — as the small size or absence of the spine on the basicerite, the stylocerite usually very large at base and ending abruptly in a sharp distal spine and the scaphocerite usually only slightly longer than the antennal blade — vary intraspecifically and are difficult to evaluate objectively.

Except for *A. estuariensis*, which has the minor first chela with the fingers about as long as the palm and similar in both sexes, the species may be divided into two groups regarding the specializations of the minor first chela: *A. euprosyne*, *A. heterochaelis*, *A. microrhynchus*, *A. paludicola* and *A. pontederiae* all have a "balaeniceps"-shaped movable finger in males, while *A. chacei*, *A. mackayi*, *A. macrodactylus*, *A. malabaricus dolichodactylus*, *A. malabaricus leptopus*, *A. malabaricus malabaricus*, *A. malabaricus songkla* and *A. tirmizae* all have fingers 1.5 to over 3 times longer than the palm.

The two groups above are probably not natural ones, as many of the remaining species of the Edwardsi group of *Alpheus* share the "balaeniceps" condition of the minor first chela in males, while in two of these species, *A. pacificus* Dana and *A. sudara* Banner & Banner, the movable finger of the minor first chela in males is both "balaeniceps"-shaped and distinctly longer than the palm (Banner & Banner, 1966).

Within the Edwardsi group of *Alpheus* the species without movable spines on the ischium of the third and fourth pereopods may form a distinct assemblage restricted to marine environments. If the fourteen specialized estuarine species of *Alpheus* are a monophyletic group, they are probably most closely related to some of the remaining species of the Edwardsi group with an unarmed merus and a movable spine on the ischium of the third and fourth pereopod, many of which are tolerant of both euhaline and eurihaline conditions.

If the above hypothesis is correct, convergent evolution with the species of the Brevirostris group of *Alpheus* must be admitted, most of which have subspatulate dactyls and a few or no spines on the propodus of the third and fourth pereopods. These morphological similarities with the estuarine species of the Edwardsi group of *Alpheus* are most probably related to similar preferences regarding the constructions of burrows in sand or mud bottoms.

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