The *Pinnixa cristata* Complex in the Western Atlantic, with Descriptions of Two New Species (Crustacea: Decapoda: Pinnotheridae)

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and

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The *Pinnixa cristata* Complex in the Western Atlantic, with a Description of Two New Species (Crustacea: Decapoda: Pinnotheridae)

*Raymond B. Manning*  
*and*  
*Darryl L. Felder*
ABSTRACT

Raymond B. Manning and Darryl L. Felder. The Pinnixa cristata Complex in the Western Atlantic, with Descriptions of Two New Species. Smithsonian Contributions to Zoology, number 473, 26 pages, frontispiece, 14 figures, 1989.—The Pinnixa cristata Complex, all members of which appear to be commensals of ghost shrimps, Family Callianassidae, or burrowing worms, comprises six species in the western Atlantic: P. aidae Righi, from Brazil; P. behreae, new species, from the northern and northwestern Gulf of Mexico; P. chacei Wass, from Alabama to the northwestern coast of Florida in the Gulf of Mexico; P. cristata Rathbun, from the Atlantic coast of the southeastern United States and from slightly variant forms from two localities in the Gulf of Mexico; P. gorei, new species, from southeastern Florida and Little Cayman Island, Caribbean Sea; and P. patagoniensis Rathbun, from Brazil to Argentina.
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Pinnixa behreae, new species, paratypes, Grand Terre (USLZ 2954): a, male, cb 7.6 mm; b, male, cb 7.8 mm. Pinnixa chacei Wass, 1955, Santa Rosa Island (USLZ 2952): c, male, cb 8.8 mm; d, female, cb 6.3 mm. Pinnixa cristata Rathbun, 1900, St. Lucie, Atlantic (USLZ 2953): e, male, cb 6.3 mm; f, female, cb 6.9 mm. Pinnixa gorei, new species, paratypes, St. Lucie, Atlantic (USLZ 2951): g, male, cb 7.2 mm; h, female, cb 7.6 mm.
The *Pinnixa cristata* Complex in the Western Atlantic, with Descriptions of Two New Species (Crustacea: Decapoda: Pinnotheridae)

* Raymond B. Manning and Darryl L. Felder

**Introduction**

In 1982, one of us (R.B.M.) initiated studies on infaunal decapods from the vicinity of the southern Indian River lagoon, eastern coast of Florida, using the Smithsonian Marine Station at Link Port, Fort Pierce, as a base of operations. One of the first areas investigated was a sand beach habitat on the Atlantic coast just north of the St. Lucie Inlet, at the southern end of the Indian River (St. Lucie site of Gore, Scotto, and Becker, 1978). Here a narrow sand flat, situated between the sand beach shore and an emergent sabellariid worm reef, was sampled several times with a commercial yabby pump, a suction pump that greatly facilitates the collection of burrowing organisms (see accounts in Hailstone and Stephenson, 1961, and Manning, 1975). Among the decapods collected at this site were two similar but distinct species of *Pinnixa*, both of which keyed to *Pinnixa cristata* Rathbun in Rathbun (1918) as well as in Williams (1965); one of the two proved to be undescribed.

Subsequent sampling by us in the Indian River from localities between Sebastian Inlet to the north and St. Lucie Inlet to the south (Figure 1) yielded numerous additional representatives of *Pinnixa*. Many of these proved to be true *P. cristata*, but no representatives of the second species or any other members of the *P. cristata* Complex were taken in other areas of the Indian River lagoon. We added other localities for the new species on the east coast of Florida when sampling was extended south to the Lake Worth Inlet and Miami. Also, collections by one of us (D.L.F.) and by Richard Heard, Gulf Coast Research Laboratory, in the northern and western Gulf of Mexico yielded additional members of the *P. cristata* Complex, including specimens of *P. cristata* proper, until now known only from the Atlantic coast of the United States, and material of a second undescribed species. The new species that we found necessitated a review of the members of the *P. cristata* Complex in the western Atlantic. The results of that review are presented herein.

**Collecting Sites Near Fort Pierce.**—Much of the material reported herein was collected in the vicinity of the Indian River lagoon, Florida, or on beaches of the adjacent Atlantic Ocean, at the following collection sites (Figure 1):

- **Sebastian South**: Indian River County, Indian River, south side of Sebastian Inlet, shallow flat with some grass at western end of inlet; 27°50.8’N, 80°27.4’W; RBM station: FP-84-2, R.B. and L.K. Manning, 8 Jul 1984.
- **Fort Pierce Inlet, Dynamite Point**: St. Lucie County, Indian River, north side of Fort Pierce Inlet; 27°28.3’N, 80°17.8’W; RBM station: FP-85-2, R.B. Manning and M.L. Reaka, 14 Aug 1985.

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FIGURE 1.—Map of area sampled on central Florida east coast, between Sebastian and St. Lucie Inlets.


Fort Pierce Inlet, causeway site: St. Lucie County, Indian River, south side of Fort Pierce Inlet, on sand flat separated from causeway by shallow (4' (=1.2 m) channel; 27°27.7'N, 80°18.7'W; RBM stations: FP-85-3, R.B. and L.K. Manning, 23 Jul 1985; FP-85-8, R.B. Manning, M.L. Reaka, W.D. Lee, and B. Tunberg, 15 Aug 1985.

Stuart Causeway: Martin County, Indian River, U.S. Highway A1A causeway from Stuart to beach, across from boat ramp, hard sand next to shore; 27°12.5'N, 80°11.5'W; RBM station: FP-84-7, R.B. Manning and D.L. Felder, 14 Jul 1984.


Lake Worth Inlet, Peanut Island site: Palm Beach County, Lake Worth, Peanut Island, tidally washed flats on north side of island, varying from clean sand to shelly sand; 26°46.7'N, 80°02.9'W; RBM stations: FP-87-8, D.L. Felder, W.D. Lee, P. Mikkelsen, and R. Bieler, 10 Aug 1987; FP-87-9, D.L. Felder and W.D. Lee, 11 Aug 1987; FP-87-10, D.L. Felder, W.D. Lee, and P. Mikkelsen, 12 Aug 1987 (site not shown on Figure 1).

Collections were made in the general area around each of these sites. Curiously, although *Pinnixa cristata* has not been recorded from localities below Hunting Island, South Carolina, it is not only one of the most common species that we have found in the Indian River but also one of the most common infaunal macrocrustaceans of the area. It shares this role with four other species of burrowing crustaceans that also are very common in the Indian River region: the callianassids *Callianassa grandimana* and *Callichirus major*, and the stomatopods *Coronis scolopendra* Lateille, 1828, and *Lyssosquilla scabricauda* (Lamarck, 1818). Except for *L. scabricauda*, reported by Gore and Becker (1976), none of these species has been recorded previously from the Indian River.

**Callianassid Associates of Pinnixa.**—The species of *Pinnixa* reported herein have been recorded previously, in some cases erroneously, as occurring together with several callianassid species. These include: the two Atlantic species of the genus *Callichirus* Stimpson, 1866, *Callichirus islagranda* (Schmitt, 1935), and *Callichirus major* (Say, 1818), recently removed from the synonymy of *Callianassa* by Manning and Felder (1986), and several species of the genus *Callianassa* Leach, 1814, sensu stricto, namely *Callianassa biformis* Biffar, 1971, *Callianassa grandimana* Gibbes, 1850 (known under its junior synonym, *Callianassa branneri* Rathbun, 1900)), and *Callianassa louisianensis* Schmitt, 1935 (= *Callianassa jamaicense* var. *louisianensis* Schmitt, 1935). Manning (1987) showed that *Callianassa grandimana* was the oldest name available for the species then known as *Callianassa branneri* (Rathbun, 1900), one of the most abundant callianassid species in the Indian River lagoon system and adjacent waters.

We also offer additions and corrections to recorded symbiotic associations in our discussion of biology under each species account.

**METHODS.**—All measurements are given in millimeters (mm). Carapace length (cl) is measured on the midline, from the front to the posterior margin of the carapace. Carapace breadth (cb) is the greatest width, measured between the lateral extremes of the carapace just above the coxae of the pereopods. A measurement given as 4.8 x 9.1 mm indicates that the specimen is 4.8 mm long, 9.1 mm wide.

Lengths of the merus and propodus of the third walking leg
are measured on the superior (dorsal) margin.

The abbreviations P-1, P-2, P-3, P-4, and P-5 refer to the first to fifth pereopods, respectively. P-1 is the cheliped, and P-4 is the third walking leg.

We use gonopod for the first pleopod of the male.

For clarity, setae often are omitted in the figures.

Coordinates given in parentheses for localities have been taken from the gazetteers of the United States Board on Geographic Names.

We use the abbreviation ppt for parts per thousand when giving water salinity.

Photo vouchers are specimens photographed live in the field by D.L. Felder.

REPOSITORIES.—Specimens have been deposited in the following collections: National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); Indian River Coastal Zone Museum, Harbor Branch Oceanographic Institution, Fort Pierce, Florida (IRCZM); Center for Crustacean Research, University of Southwestern Louisiana, Lafayette (USLZ); the Marine Environmental Sciences Collection (MESC) of the Dauphin Island Sea Laboratory, Dauphin Island, Alabama; and the British Museum (Natural History), London (BM).

ACKNOWLEDGMENTS.—This study was carried out at the Smithsonian Marine Station at Link Port, Fort Pierce, Florida. This is Contribution number 164 from the Smithsonian Marine Station at Link Port, Fort Pierce, Florida (IRCZM); Center for Crustacean Research, University of Southwestern Louisiana, Lafay-
ette (USLZ); the Marine Environmental Sciences Collection (MESC) of the Dauphin Island Sea Laboratory, Dauphin Island, Alabama; and the British Museum (Natural History), London (BM).

We gratefully acknowledge the aid of W.D. Lee in the field and laboratory. We are indebted to S.A. Rodrigues, Universidad de Sao Paulo, for providing us with specimens of *Pinnixa aidae* and *P. patagoniensis*, material that resolved many questions for us. M. Turky, Forschungsinstitut Senckenberg, Frankfurt am Main, Germany, loaned one of us (R.B.M.) the types of *Pinnixa salvadorensis* Bott, for which we thank him. We thank Jennifer M. Felder, who measured most of the specimens for us, Lilly King Manning, who drew many of the figures and prepared all figures for publication, and Austin B. Williams, National Marine Fisheries Service Systematics Laboratory, and Richard W. Heard, Gulf Coast Research Laboratory, who reviewed the manuscript. Dr. Heard also provided us with specimens and literature, and shared with us his material of *Pinnixa cristata* from the northern Gulf of Mexico. M. Dardeau, Dauphin Island Sea Laboratory, and J.W. Martin, Florida State University, made specimens available from their respective institutions, for which we thank them. E.E. Bosch, Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata, Argentina, helped us obtain references. Paul Clark, British Museum (Natural History), loaned us material from Little Cayman Island. Figures 6 and 13 were prepared by Jack Schroeder for the late Waldo L. Schmitt. Molly Kelly Ryan corrected Figure 6 to our specifications.

Family PINNOTHERIDAE de Haan, 1833

Genus *Pinnixa* White, 1846

*Pinnixa* White, 1846:33. [Type species *Pinnotheres cylindricum* Say, 1818, by monotypy. Gender: feminine.]

WESTERN ATLANTIC SPECIES of *Pinnixa*.—The two new species described herein raise the total number of described species in the western Atlantic to 22, as follow (species treated by Williams, 1984, are preceded by an asterisk):

*Pinnixa aidae* Righi, 1967
*Pinnixa arenicola* Rathbun, 1922
*Pinnixa behreae*, new species
*Pinnixa brevipollex* Rathbun, 1898
*Pinnixa chacei* Wass, 1955
*Pinnixa chaetopterana* Simpson, 1860
*Pinnixa cristata* Rathbun, 1900
*Pinnixa cylindrica* (Say, 1818)
*Pinnixa faxonii* Rathbun, 1918
*Pinnixa floridana* Rathbun, 1918
*Pinnixa garlhi* Fenucci (1975:169)
*Pinnixa gorei*, new species
*Pinnixa leptomysia* Wass, 1968
*Pinnixa luizi* Glassell, 1937
*Pinnixa minuta* Rathbun, 1901
*Pinnixa monodactyla* (Say, 1818)
*Pinnixa patagoniensis* Rathbun, 1918
*Pinnixa pearsei* Wass, 1955
*Pinnixa rapax* Bouvier, 1917
*Pinnixa retina* Rathbun, 1918
*Pinnixa sayana* Simpson, 1860
*Pinnixa vanderhorstii* Rathbun, 1922

Original references as well as citations for most of these species can be found in Schmitt, McCain, and Davidson (1973). The original reference for *Pinnixa garlhi*, the only western Atlantic species described since 1973, is cited above.

The *Pinnixa cristata* Complex.—Members of this complex can be recognized by the presence of a high, sharp, uninterrupted transverse crest across the posterior margin of the carapace. This feature allows the separation of these species from all other American species of the genus in the first couplet of the key to American species of *Pinnixa* given by Rathbun (1918:129), as well as in the key to Carolinian species provided by Williams (1984:450). In addition, the carapace of these species is very short (cb 1.8 to 3.3 times cl), the third walking leg (P-4) is much the largest of the walking legs, and the abdomen is composed of 7 free somites in both sexes. All of these species are relatively small, with the carapace length not exceeding 6.0 mm, and all appear to live as commensals with callianassid ghost shrimps and possibly other burrowing organisms as well.

In addition to the species characterized herein, the *Pinnixa cristata* Complex includes one Eastern Pacific species, *P. felipensis* Glassell (1935:14), described from the Gulf of California, Mexico. *Pinnixa salvadorensis* Bott (1955:59), from Coral de Mulas and La Cepona, El Salvador, is a synonym.
of *P. felipensis*; one of us (R.B.M.) compared the types of the two species.

During the course of this study it has become apparent that several easily discernible characters are diagnostic in this group of species. These include the presence (e.g., in most species) or absence (e.g., in *P. aidae* and *P. gorei*, new species) of a branchial ridge, whether it extends to the orbit (as in *P. patagoniensis* but not in other species), and its configuration. The ridge in *P. chacei* and *P. behreae*, new species, extends laterally from near the orbit but makes a sharp bend to the rear before reaching the lateral margin; in other species that have the ridge it is more or less evenly curved toward the lateral margin. Four species, *P. aidae*, *P. behreae*, new species, *P. chacei*, and *P. patagoniensis*, show a short but distinct ridge extending mesially from each orbit; these ridges are replaced by a low, indistinct boss in *P. cristata* and *P. gorei*, new species.

The fourth pereopod provides several diagnostic features: the opposable margin of the propodus may be bicarinate (most species) or single (*P. chacei*, *P. gorei*, new species), and the dactylus may be longitudinally ridged on its posterior surface, strongly so as in *P. behreae*, new species, *P. chacei*, and *P. patagoniensis*, or less conspicuously, as in *P. cristata*; in two species (*P. aidae*, *P. gorei*, new species) the ridges are not discernible. The dactylus is ventrally grooved in all of the species reported herein.

Finally, the shape of the gonopod can be diagnostic: examination of the gonopod in a range of specimens originally identified as *P. chacei* allowed us to recognize *P. behreae*, new species, as a distinct species.

We provide here a key to the Atlantic members of this distinctive group of species of *Pinnixa*.

### Key to Western Atlantic Species of the *Pinnixa cristata* Complex

1. Carapace without branchial ridges [Figure 2a,b]. (P-4 dactylus without longitudinal ridges on anterior and posterior surfaces [Figure 2g].) .................................................. 2

2. Carapace with distinct ridge on each branchial region [Figure 3a,b] ............................................. 3

3. Opposable margin of P-4 propodus bicarinate [Figure 2g] ............................................. *P. aidae*

4. Opposable margin of P-4 propodus with single carina [Figure 11e] ................................. *P. gorei*, new species

5. Branchial ridges each extending to orbit [Figure 13]. (P-4 dactylus with distinct longitudinal ridges on anterior and posterior surfaces [Figure 14c].) .................................................. *P. patagoniensis*

6. Branchial ridges falling short of orbit .................................................................................. 4

7. Branchial ridges extending laterally or gently curved towards posterior, lacking sharp bend laterally [Figure 6] ............................................. *P. cristata*

8. Branchial ridges angled laterally, with sharp bend toward posterior [Figure 3a,b] .................................................. 5

9. Opposable margin of P-4 propodus with single carina [Figure 5f]. Gonopod with truncate apex [Figure 5h–k]. (P-4 dactylus with low longitudinal ridge on posterior surface only.) ................................. *P. chacei*

10. Opposable margin of P-4 propodus bicarinate [Figure 3g]. Gonopod with hooked, styliform apex [Figure 4]. (P-4 dactylus with strong longitudinal ridge on anterior and posterior surfaces.) ............................................. *P. behreae*, new species

### *Pinnixa aidae* Righi, 1967

![Figure 2](image)


**Diagnosis.**—Carapace 2.2 to 2.5 times broader than long in adults, with high, sharp, cardiac crest extending from side to side above posterior margin. No transverse ridge on branchial region. A carina extending mesially from each orbit, interrupted medially.

Chelipeds of male and female similar, both with deflexed movable fingers on chelae. Chela of male inflated, longer than that of female, fixed finger almost as long as palm, unarmed. Movable finger of male chela deflexed, but not so sharply as in *P. patagoniensis*, unarmed, gape obscured by setae. Chela of female with broad, low, rectangular tooth on fixed finger, cutting edge of movable finger sinuous but not distinctly toothed, gape obscured by setae.
Third walking leg (P-4) strongest, merus 2.1 to 2.2 times longer than high, lower posterior surface densely setose. Propodus 1.4 to 1.5 times longer than high, ventral (opposable) surface bicarinate. Dactylus lacking longitudinal ridge on anterior and posterior surfaces.

Male abdomen and gonopod as figured by Righi (1967, figs. 23, 24; sex incorrectly indicated; Figure 2i herein). Seventh somite of male abdomen longer than sixth.

SIZE.—Only one ovigerous female examined, cl 4.7 mm, cb 11.2 mm. Measurements recorded in the literature: ovigerous female, cl 3.8 mm, cb 8.5 mm; male, cl 4.2 mm, cb 10.7 mm (rounded from Righi, 1967).

COLOR IN LIFE.—Not recorded.

REMARKS.—*Pinnixa aidae* resembles *P. gorei* and differs from all other Atlantic members of the *Pinnixa cristata* Complex in lacking a distinct ridge on each branchial region. It can be distinguished from *P. gorei* by the structure of the ventral (opposable) margin of the propodus of the fourth pereopod: in *P. aidae* that margin is bicarinate, whereas it has a single carina in *P. gorei*. 

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**Figure 2.**—*Pinnixa aidae* Righi, 1967: a, dorsal view; b, carapace; c, third maxilliped; d, cheliped of male; e, f, chelipeds of female; g, P-4; h, abdomen of male; i, gonopod. a, c–e, i from Righi, 1967; b, f–h, female, cb 11.2 mm, Praia do Araça.
Biology.—No associates have been recorded for this species. Righi (1967) recorded it and *P. patagoniensis* from the Enseada de Caraguatatuba.

Ovigerous females have been collected in May (present paper) and in November (Righi, 1967).

Distribution.—Known only from shallow water along beaches at two localities in the State of São Paulo, Brazil.

**Pinnixa behreae**, new species

_Frontispiece, Figures 3, 4_

*Pinnixa* sp.—Behre, 1950:25.


*Pinnixa cristata*.—Phillips, 1971:181 [part, others may be *Pinnixa cristata* Rathbun, 1900.]


Material.—Alabama: Dauphin Island, western end, Mississippi Sound (landward) side; overwash fan of sand over mud, intertidal, night, with *Callichirus islagrande*; 1 Aug 1985; D.L. Felder and M. Dardeau; 1 male (MESQ.1985). Mustang Island; Gulf beach 4 miles from jetty; intertidal zone; 26 Nov 1954; H. Hildebrand; 1 male, 1 damaged specimen (USNM 99829). Bob Hall Pier, north of Malaquite Beach, Padre Island; with *Callichirus islagrande*; 26 Jun 1977; Ray Allen; 28 males, 27 females (4 ovigerous) (USLZ 2957). Padre Island National Seashore, about 55 miles south of park headquarters, Kenedy County; 1 Jul 1974; A.H. Chaney and class; 1 male (USLZ 2620).

All specimens other than the holotype are paratypes.

Diagnosis.—Carapace 1.9 to 3.0 (mean 2.6, based on 31 specimens larger than cb 6.0 mm) times broader than long in adults, with high, sharp cardiac crest extending from side to side above posterior margin. Branchial regions each crossed by low, tuberculate ridge, not extending to orbit; laterally, ridge turning sharply towards posterior, falling short of posterolateral margin. A distinct, short ridge extending mesially from each orbit, interrupted medi ally.

Chelipeds of males and females dissimilar, those of male larger. In male, chela stout, distal margin of palm almost perpendicular, with broad, rectangular median tooth, gape very slight above tooth. Fixed finger very short, with subdistal area unarmed, cutting edge serrate. Chelae of females with both fingers extended, like those of juveniles. Female chela with fixed finger much larger than in male, elongate, neither finger toothed.

Third walking leg (P-4) strongest, merus 1.9 to 2.2 times longer than high, lower margin fringed with few setae, posterior face otherwise naked or nearly so. Propodus 0.9 to 1.1 times longer than high, ventral (opposable) surface bicipinate, posterior carina positioned well onto posterior surface of propodus, higher and smoother than anterior carina. Dactylus with strong longitudinal ridge on anterior and posterior surfaces.

Male and female abdomen of 7 free somites. First somite of male abdomen trapezoidal, only slightly wider than second. Articulation between second and third somites produced slightly, with angle laterally. Abdomen tapering to sixth somite, telson subcordiform, much narrower and shorter than sixth somite.
Gonopod as illustrated (Figure 4), apex hooked, styliform.

SIZE.—Males, cl 1.3 to 4.8 mm, cb 2.5 to 9.1 mm; non-ovigerous females, cl 1.7 to 2.6 mm, cb 3.5 to 7.1 mm; ovigerous females, cl 2.0 to 3.5 mm, cb 4.5 to 8.6 mm.

The largest specimen examined is the male holotype; it measures 4.8 x 9.1 mm.

COLOR IN LIFE.—Chelipeds diffuse white to translucent, white sometimes concentrated on merus and on superior surfaces of carpus and manus. Walking legs largely translucent, except for white areas of varying intensity, especially on distal parts of carpus and propodus. P-4 sometimes with white well developed on distal part of merus, over most of carpus, and at proximal and distal extremes of propodus.

Dorsal pattern of carapace varying between two extremes, one dominated by white chromatophores, other dominated by dark grey to black chromatophores, either appearing to be
faintly marbled with traces of translucent tan. Intermediate carapace patterns usually dominated by translucent tan, with white sometimes developed at lateral extremes.

Margins, ridges, and setae of carapace and appendages often fouled to varying degrees by dark brown to black precipitate or deposit.

**REMARKS.**—Until now material of this species had been identified with *P. chacei* Wass, a species that was believed to range from the coast of Florida to Texas in the northern Gulf of Mexico. Examination of the gonopods of males from several localities revealed the existence of two similar but distinct species along the American coast of the Gulf of Mexico, one, *P. chacei*, apparently restricted to northwestern Florida and Alabama, the other, *P. behreae*, new species, occurring from Alabama to Texas.

*Pinnixa behreae* agrees with *P. chacei* and differs from all other Atlantic members of the *Pinnixa cristata* Complex in having a sharp bend to the posterior in the lateral part of the branchial ridge, which forms a near right angle on each side of the carapace. *Pinnixa behreae* differs from *P. chacei* in having the ventral (opposable) margin of the fourth pereopod distinctly bicarinate; in *P. chacei* the ventral margin of the propodus of the fourth leg has but a single carina. Further, the gonopod is distinctly different in males of the two species, being blunt apically in *P. chacei*, but with a hooked, styliform tip in *P. behreae*. In females of *P. behreae*, the chela has a dense tuft of setae in the gape; in *P. chacei* the female has few setae in the gape of the chela.

Chelae of immature males of *P. behreae* resembling those of the females, with the fingers extended, including the presence of the dense tuft of setae in the gape. Immature specimens of both sexes have the posterior carina on the propodus of P-4 weakly developed.

**ETYMOLOGY.**—We are pleased to dedicate this species to the late Elinor H. Behre, a pioneer of marine science studies in the Gulf of Mexico.

**BIOLOGY.**—This species appears to preferentially inhabit burrows of the callianassid *Callichirus islagrande*, often in habitats where salinity may fall periodically to 10 ppt or less. However, one of us (D.L.F.) has taken it occasionally from burrows of *Callichirus major* on the Louisiana coast, in areas where these two species occur together. The following information on biology has been recorded in the literature: Behre (1950:26) noted that it was “never in oyster shells.” Hedgpeth (1950:116) remarked that “one pinnixid crab was taken in a seine haul.... The salinity was 14.0 %c.” Felder (1973:71) reported that it is “found as commensal with *Callianassa islagrande* in intertidal zone of sandy Gulf beaches,” and (p. 74) that it is “known from intertidal beaches and shallow sand and sandy-mud bottoms in brackish to marine waters; usually commensal with callianassids or other burrowers.” According to Powers (1977:125), this species is “intertidal, commensal with burrowing shrimp, *Callinassa* [sic] *islagrande*, living in upper part of burrows; on sandy bottoms.” Phillips (1971:181) commented:
Burrows of both Mississippi Sound mudshrimps harbored pinnixid crabs (Pinnixa (sic) cristata Rathbun), about one to five crabs per burrow. The Pinnixa (sic) inhabiting islagrande burrows exhibited considerable polymorphism with respect to coloration. Those infesting jamaicense burrows were uniformly black and were covered with a dense hydroid growth. The significance of the pinnixid polymorphism is unclear, but it is probably related to substrate.

So far as we know, Phillips provided the only record of an association between a member of the Pinnixa cristata Complex and Callianassa louisianensis (= Callianassa jamaicense var. louisianensis Schmitt, 1935). His observation requires verification; to date we have not observed this association even though one of us (D.L.F.) has collected several thousand specimens of C. louisianensis along the Louisiana coast over the last 10 years. It should be noted that Phillips’ collections were in an area where both P. behreae and the only known northern Gulf population of P. cristata occur in close proximity. While his comments on color polymorphism for associates of Callichirus islagrande almost certainly refer to P. behreae, it is likely that the “uniformly black” specimens found by him to be associated with other burrows were P. cristata. We question the identification of those burrows with Callianassa louisianensis.

Ovigerous females have been taken in June, July, and August (present material and Wass, 1955). DISTRIBUTION.—Northern Gulf of Mexico, from Alabama to Texas. Usually intertidal, occasionally to a depth of several meters.

**Pinnixa chacei** Wass, 1955

**FRONTISPIECE, FIGURE 5**


**MATERIAL.—Florida:** Outer beach of Alligator Point, Franklin County; from Callianassa burrows; 4 Oct 1952; M.L. Wass; 5 males (paratypes, USNM 98905). Same data; 1 male (holotype, USNM 95694). Same data; 1 female (allootype, USNM 205683). Gulf beach across from marine lab, Alligator Point; 30 Aug 1952; M.L. Wass; 7 females (2 ovigerous) (paratypes, USNM 95695). Kevins Beach, Highway 98, east of Florida State University Marine Laboratory; 12 Jun 1987; K. Carmen and F. Dobbs; 1 female (USLZ 1963). From Callichirus burrows, immediately east of Florida State University Marine Laboratory; J. Martin and F. Dobbs; 1 male, 1 female (USLZ 2964). Ft. Pickens end of Gulf Beach, Santa Rosa Island, Pensacola; from burrows of Callichirus islagrande; 10 Oct 1980; D. Felder and R. Heard; 12 males, 13 females (USLZ 2952; largest specimens are photo vouchers).

**Alabama:** Dixie Bar, off Mobile Bay east of Dauphin Island; bucket dredge on sand bar in 1 m depth; 20 Jan 1977; M. Dardeau; 2 males (MESC).

**DIAGNOSIS.—**Carapace 1.8 to 2.9 (mean 2.3, based on 17 specimens larger than cb 5.0 mm) times broader than long in adults, with high, sharp cardiac crest extending from side to side above posterior margin. Branchial regions each crossed by distinct tuberculate ridge, not extending to orbits, laterally with sharp turn to posterior, extending almost to posterolateral margin. Distinct ridge extending mesially from each orbit, diminished or interrupted along midline.

Chelipeds of male and female dissimilar, those of male larger. In male, distal margin of palm almost perpendicular, with broad, rectangular median tooth; gape setose above tooth. Fixed finger very short, deflexed, distally serratte. Dactylus strongly deflexed, lacking distinct tooth, distally serratte on opposable margin. Female chela like that of juveniles, fingers extended, cutting edges serratte but lacking distinct teeth, few setae in gape.

Third walking leg (P-4) strongest, merus 1.1 to 2.3 times longer than high, lower margin fringed with setae, posterior face otherwise naked. Propodus about 1.2 to 2.5 times longer than high, ventral (opposable) margin with single carina. Dactylus with low but distinct longitudinal ridge on posterior face, anterior face lacking ridge.

Male and female abdomens with 7 free somites. Male abdomen with first somite trapezoidal, wider than second, tapering slightly from second to fifth somites, corners of somites not markedly produced at articulations. Sixth somite with sides concave. Telson broader and longer than sixth somite, cordiform, widest posterior to base.

Gonopod as illustrated (Figure 5h–k), apex blunt.

**SIZE.—**Males, cl 1.7 to 3.5 mm, cb 4.5 to 8.9 mm; non-ovigerous females, cl 1.5 to 2.7 mm, cb 4.1 to 6.3 mm; ovigerous females, cl 2.2 to 2.6 mm, cb 5.6 to 6.0 mm.

The largest specimen examined is a male measuring 3.5 × 8.9 mm.

**COLOR IN LIFE.—**“In life, males white, with brown specking; females slate grey, with translucent legs; juveniles paler” (Wass, 1955:161). Color very similar to that of *P. behreae* in pattern and variation. Chelipedes diffuse white to translucent, white sometimes concentrated on merus and carpus, sometimes extending to superior and distal areas of manus. Walking legs largely translucent to diffuse white, white areas when developed usually confined to distal or superodistal extremes of carpus and propodus.

Dorsal pattern of carapace varying between two extremes, one dominated by white chromatophores, the other by dark grey to black chromatophores, with intervening areas appearing as traces of translucent tan.

**REMARKS.—**This species resembles *P. behreae* and differs from all other members of the *Pinnixa cristata* Complex in
having the ridge on the branchial region turning sharply toward the posterior, forming a distinct angle laterally. Other differences are mentioned under the account of *P. behreae*.

**Biology.**—Like *P. behreae*, this species lives in association with *Callichirus islagrande*. Wass (1955:161) noted that it occurred in the "intertidal zone; commensal with *Callianassa islagrande*, living in the upper part of the fragile sand-walled burrows." Menzel (1956:81) noted that it is "comm[ensal]."
with Call. islagrande [sic]."

We have found this species to be particularly common along wave-washed beaches of clean sand that front or form terminal spits on the barrier islands of western Florida. Here P. chacei occurs in burrows of Callichirus islagrande that are concentrated on the lower intertidal beaches and in shallow troughs between subtidal sand bars. Chimneys of the host's burrows may be exposed here by wave erosion of surrounding sand, and the commensal P. chacei may sometimes be observed just inside the narrow opening of the host's burrow.

Our record of this species from Alabama waters suggests that the habitat of P. chacei extends well onto shallow subtidal sandbars, and raises the possibility that P. chacei and P. behreae may be sympatric along part of the northern Gulf coast.

Ovigerous females have been collected in August and October (present material and Wass, 1955).

**DISTRIBUTION.**—Apparently restricted to the northeastern Gulf of Mexico, from near Apalachee Bay, Florida, to Alabama. Usually intertidal, occasionally to a depth of several meters.

**Pinnixa cristata** Rathbun, 1900

**Frontispiece, Figures 6-9**


*Pinnixa chaetopoterana*.—Phillips, 1971:181 [part? questionable record, at least part see P. behreae, which see].

*Pinnixa chaetopoterana*.—Howard and Dörjes, 1972, fig. 14 [not P. chaetopterana Stimpson, 1860].

**PREVIOUS RECORDS.**—ATLANTIC OCEAN.

**North Carolina:** Beaufort (Rathbun, 1900; Hay and Shore, 1918; Rathbun, 1918; Pearse, Humm, and Wharton, 1942; Williams, 1965, 1984). **South Carolina:** North Inlet (Young, 1978). Edisto Island (Williams, 1965, 1984). Huntington Beach, Debideu Flat, Folly Beach, Breach Inlet, and Hunting Island (Fox and Ruppert, 1985). **Georgia:** Cabretta flat, Sapelo Island (Howard and Dörjes, 1972; Dörjes, 1972). **Florida:** Florida (Abele and Kim, 1986).

**GULF OF MEXICO.** **Mississippi:** Horn Island (Phillips, 1971) (probably specimens described as "uniformly black"; see above under account of *P. behreae*).

**MATERIAL.**—ATLANTIC OCEAN. **North Carolina:** Beaufort; Union College Collection; 1 female (holotype, USNM 42817). Beaufort, Fort Macon Beach; in worm tube; 6 Jul 1939; A.S. Pearse; 1 ovigerous female (USNM 155241). Beaufort, Sheepshead Shoal; in Callichirus major tube; 2 Aug 1939; 1 male, 1 ovigerous female (USNM).

**South Carolina:** Isle of Palms; washed on beach; 7 Jan 1936; G.R. Lunz, Jr.; 3 males, 1 female (USNM 74962). Edisto Island; from hole in beach, perhaps of annelid?; C.H. Townes; 3 males, 2 ovigerous females, 1 juvenile (USNM 74961).

**Georgia:** South end of Tybee Island, Chatham County; 26 Jul 1980; R.W. Heard; 6 males, 17 females (11 ovigerous), 10 juveniles (USNM). Tybee Island, 10th St. beach; from burrows of Callichirus major; 16 Apr 1988; G.A. Bishop; 11 males, 27 females (25 ovigerous) (USNM).

**Florida:** St. Augustine Beach; with Callichirus major; 20 Sep 1980; R.W. Heard; 12 males, 15 females (13 ovigerous) (USNM). South Melbourne Beach, Brevard County; 90 m from shore, in 2 m; 20 Jan 1980; T. Roberts; 1 male (IRCSZM 089:04700). South Melbourne Beach, Brevard County; ~90 m from shore, off Air Force tracking station; 6-inch (= 15 cm) PVC corer; 11 Apr 1980; K. Spring; 1 male (IRCSZM 089:05113).

Fort Pierce Sites, Sebastian North: Sta. FP-84-3, 1 male, 1 female (USNM); Sta. FP-84-9, 4 males, 4 ovigerous females (USLZ 2958).

Sebastian South: Sta. FP-84-2, 1 male, 1 female (USNM). Fort Pierce Inlet, Dynamite Point: Sta. FP-85-6, 1 male, 1 female (USNM).

Fort Pierce Inlet, Coon Island: Sta. FP-85-2, 7 males, 9 females (5 ovigerous)(USNM).

Fort Pierce Inlet, north side: Sta. FP-84-5, 3 males, 4 females (1 ovigerous)—2 specimens taken with Callichirus major (USNM); Sta. FP-84-11, 2 males (USNM).

Stuart Causeway: Sta. FP-84-7, 1 ovigerous female (USNM).

St. Lucie, Indian River: Sta. FP-82-8, 2 males, 1 female (USNM); Sta. FP-83-2, 2 males, 1 ovigerous female (IRCSZM 089:06323); Sta. FP-83-4, 7 males, 4 females (1 ovigerous)—2 specimens taken with Callichirus major (USNM).

St. Lucie, Atlantic: Sta. FP-82-3, 8 males, 7 females (7 USNM); Sta. FP-82-5, 1 male, 1 female (USNM); Sta. FP-82-7, 3 males (USNM); Sta. FP-83-3, 2 males, 1 female—1 specimen taken with Callianassa grandimana (USNM); Sta. FP-83-6, 3 males, 5 females—1 specimen taken with Callichirus major, 1 specimen taken with Callianassa grandimana (USNM); Sta. FP-84-1, 6 males, 5 females (1 ovigerous)—2 specimens taken with Callichirus major (2 males, 4 females IRCSZM 089:06324, remainder USNM); Sta. FP-84-4, 15 males, 8 females—3 specimens taken with Callichirus major, 1 specimen taken with Callianassa grandimana (2 males, 3 females, including photo vouchers, USLZ 2953, remainder USNM); Sta. FP-85-3, 21 males, 29 females (3 ovigerous), 3 juveniles (10 males, 14 females USLZ 2959, remainder USNM).

Lake Worth Inlet, Peanut Island: Sta. FP-87-8, 2 males, 3 females (1 ovigerous) (IRCSZM 089:06392); Sta. FP-87-9, 2 males, 1 female (IRCSZM 089:06394); Sta. FP-87-10, 3 males, 3 females (2 ovigerous) (IRCSZM 089:06393).

Dade County, Key Biscayne, southeastern side of Bear Cut at marina: Sta. RBM Miami-4, sand flat exposed at low tide;
yabby pump; 1 male (USNM); R.B. Manning; 23 May 1988.

GULF OF MEXICO. Mississippi: Horn Island, Sta. 2, yabby pump on sand flat, north side of island; 1–1.5 m deep; with Callichirus major; 9 Jul 1987; R.W. Heard; 6 males, 4 females (1 ovigerous) (USNM).

MEXICO. State of Tamaulipas: Village of Barra del Tordo, estuary at mouth of Río Carrizal, 23°03′N, 97°46′W, collected using yabby pump, from grass bed burrowed by worms and thalassinids; 25 May 1982; D.L. Felder and R. Tinnin; 2 males (USNM 221633).

DIAGNOSIS.—Carapace 2.1 to 3.3 (mean 2.6, based on 143 specimens larger than cb 5.0 mm) times broader than long in adults, with high, sharp cardiac crest extending from side to side above posterior margin. Branchial regions each crossed by tuberculate ridge, mesially not extending to orbit, not angled laterally. No sharp carina present between orbits, replaced by low, tear-shaped transverse elevation on each side, sometimes tuberculate.

Chelipeds of males and females similar, those of males larger. In male, chela stout, distal margin of palm almost perpendicular, with very narrow but elongate tooth near middle, gape densely setose above tooth, lightly setose below. Fixed finger very short, deflexed, truncate, unarmed. In female, movable finger less deflexed, fixed finger slightly larger, each with triangular tooth, gape filled with setae.

Third walking leg (P-4) strongest, merus 2.4 to 2.9 times longer than cl. Lower part of posterior surface of merus with short but dense coat of setae. Propodus 1.3 to 1.4 times longer than high, ventral (opposable) margin distinctly bicornate. Dactylus usually lacking conspicuous longitudinal ridges on anterior and posterior surfaces, ridges occasionally present, most distinct distally.

Male and female abdomens of 7 free somites. First somite trapezoidal, slightly wider than second, articulation of somites 2–3 and somites 3–4 variably produced laterally, usually rounded, occasionally angular. Sixth somite with concave sides. Telson no wider than sixth somite, but longer, apex broadly rounded.

Gonopod as illustrated (Figures 8f–m, 9h–l).

SIZE.—Males, cl 1.3 to 3.6 mm, cb 2.4 to 10.1 mm; non-ovigerous females, cl 1.8 to 4.0 mm, cb 4.0 to 10.1 mm; ovigerous females, cl 2.6 to 3.6 mm, cb 6.5 to 9.7 mm; juveniles, cl 1.1 to 1.7 mm, cb 2.1 to 3.2 mm.

The largest specimens examined are a male, 3.2 × 10.1 mm, and a female, 3.6 × 10.1 mm. Hay and Shore (1918) and Rathbun (1918) gave the measurements of the holotype as 4.3 × 10 mm and 4.0 × 10.5 mm, respectively. Williams (1984) reported a male 3.5 × 9.1 mm and a female 4 × 11 mm. Fox and Ruppert (1985) gave 11 mm as the size of the species.

COLOR IN LIFE.—Dorsal pattern varying between two extremes: in one, background color translucent yellow or tan, with scattering of dark grey or sometimes ivory-yellow chromatophores, dactyls and extremities of propodi on walking legs translucent to faintly whitened; in other extreme, overall pattern much darker, grey to brown or dark olive, and sometimes nearly black, often with white spot on anterior slope of branchial region about halfway between orbits and lateral border of carapace, lateral border usually marked by translucent white patch; dactyls and extremities of walking legs translucent white; white color especially evident on P-4, where propodus is dark on proximal two-thirds, white on distal third.

Williams (1984:453) noted that this species shows two
distinct color patterns off North Carolina. Fox and Ruppert (1985) commented that the species has an oval dark grey carapace.

REMARKS.—*Pinnixa cristata* is a distinctive species, readily distinguished from the other Atlantic members of the genus that share the transverse crest crossing the posterior part of the carapace. It differs from *P. aidae* and *P. gorei*, new species, in having a distinct ridge across each branchial region. Unlike
**P. cristata**, *Pinnixa patagoniensis* has branchial ridges extending to the orbit and the dactyli of the fourth pereopod bearing distinct anterior and posterior ridges. *Pinnixa cristata* differs from the similar *P. chacei* and *P. behreae*, new species, in that the branchial ridges are not bent sharply towards the posterior; both of these other species had been identified with *P. cristata* in the past.

*Pinnixa cristata* is the commonest species of the genus in intertidal and shallow subtidal habitats we have sampled around Fort Pierce, Florida. It does not appear to be so common in the northern Gulf of Mexico, where the only known population occurs in shallow subtidal waters on the inshore side of Horn Island, Mississippi. That population appears to be conspicuously different from those occurring on the southeastern coast of the United States in the Atlantic, and shows some evidence of morphological divergence. In general, the specimens from Mississippi appear to be slightly coarser in overall tuberculation and to have a slightly more elongate propodus of the third walking leg (P-4) than do Atlantic populations. Development of ridges and grooves on appendages is slightly stronger in the northern Gulf population, and males from Mississippi appear to have slightly heavier gonopods. At the apex of the gonopods, the bifurcation between the abdominal and sternal lips is narrower in males from Mississippi than it is in males from Fort Pierce; in males from Mississippi the bifurcation, viewed on end, tends to be U-shaped, whereas in males from Fort Pierce the bifurcation appears to be more V-shaped. Otherwise, general sculpture and observed variation in gonopod tips were similar in Gulf and Atlantic populations. Given the subtle nature of morphological
Figure 9.—*Pinnixa cristata* Rathbun, 1900, Barra del Tordo: *a*, dorsal view; *b*, carapace; *c*, front; *d*, third maxilliped; *e*, chela; *f*, P.4; *g*, abdomen; *h–l*, gonopods: *h–j*, left, sternal face; *k,l*, left, abdominal face. *a*, male, cb 5.7 mm; *b–l*, male, cb 6.4 mm. (Arrows indicate sternal lobe of gonopod.)
differences observed between these populations, including the similarity in gonopod structure, we conclude that the Gulf population cannot be recognized as distinct from that in the Atlantic, at least on the basis of materials presently available to us.

We also assign two specimens from Barra del Tordo, Mexico, to *P. cristata*. Although the material from Mexico resembles other populations of *P. cristata* rather closely, it differs as follows: The interorbital boss is somewhat more produced to form a tuberculate ridge (Figure 9b,c); in other populations of *P. cristata* this boss is a low, poorly defined mound visible only when the surface is dried. The articular margins of the male abdomen are more sharply produced laterally (Figure 9g); they are noticeably less produced in material from other areas. Whereas males of all populations have a characteristic, moderately produced sternal lobe on the apex of the gonopod (arrows, Figure 8i, j), males of the Mexican population tend to have the abdominal lobe more produced (arrows, Figure 9i, l). This lobe is weak or absent in the Atlantic populations, occasionally developed in the northern Gulf population. Finally, the branchial ridges are much weaker on the Mexican specimens, and the longitudinal ridge on the posterior surface of the dactylus of the third walking leg (P-4) appears to be somewhat more developed.

In very large specimens of the Atlantic populations the branchial ridges may be very low and poorly developed. The longitudinal ridge on the posterior surface of the dactylus of the third walking leg is occasionally present, but it is never as well defined as in *P. patagoniensis* or *P. chacei*; in many specimens it is scarcely or not at all developed.

Coelho (1970) and Coelho and Ramos (1972) reported *Pinnixa cristata* from off Cabo de Norte, Brazil, on muddy bottom in 23 m. We tentatively identify their records with *P. patagoniensis*, as there are no other records of *P. cristata* from south of southeastern Florida. *Pinnixa patagoniensis* has been recorded from as deep as 130 m, whereas *P. cristata* appears to be restricted to intertidal and shallow subtidal habitats.

**Biology.**—There is relatively little information in the literature on the biology of this species. Pease, Humm, and Wharton (1942:186) noted that it was “rather common on sand flats, in various worm tubes, and in Callianassa burrows.” MacGinitie and MacGinitie (1949:316) and (1968:316) noted: “On the East Coast the pea crab *Pinnixa cristata* that occurs with *Callianassa* is also found in worm tubes.” Young (1978:183) reported its habitat as sandy beaches. Williams (1965:210) noted that “the species has been taken from sandy beaches by digging and sifting in North Carolina and South Carolina.” Williams’ other comments and his later comments (1984:453) refer to Gulf species, not *P. cristata*.

Fox and Ruppert (1985) mentioned the species several times in their survey of benthiic macroinvertebrates of South Carolina. They reported (pp. 37, 40) that at Huntington Beach, a northern, outer, protected beach, it was common in spring and summer, and it was associated with *Callichirus major*; at Debidue Flat (p. 52), a northern protected beach, it was uncommon in summer and winter; at Folly Beach (p. 115), a central outer beach, it was common in spring and summer; at Breach Inlet (pp. 122, 129), a central protected beach, it was common, perennial, and occurred with *Callianassa setiferus* (DeKay, 1844) as *C. atlantica* Rathbun, 1926; possibly meaning *Callianassa biformis*, the inshore counterpart of *C. setiferus*. This record almost certainly refers to another species of *Pinnixa*, one occurring with either *C. biformis* or *C. setiferus*; and at Hunting Island (p. 187), a southern, outer beach, it was common and perennial, occurring with *Callianassa*.

Howard and Dörjes (1972) reported this species as an associate of *Callichirus major* at Sapelo Island, Georgia; they referred to it under both *P. chaetopterana* and *P. cristata*. According to R.W. Heard, who brought this reference to our attention, part of their material of “*P. chaetopterana*” is referable to *P. cristata*, part to a new species of *Pinnixa*.

In samples from the Fort Pierce area, *P. cristata* was taken from intertidal and shallow subtidal sandy beaches and flats, most commonly in association with *Callianassa grandimana* and *Callichirus major*, and it appears to exhibit no preference between these species. In Lake Worth it appeared to occur as well with *Callianassa guassutinga* Rodrigues, 1971. We have not taken it with any other species of callianassid in the Fort Pierce area, and we have not taken it in association with burrowing worms, although many specimens were taken from burrows of unknown origin. Likewise, the specimens we report from Horn Island, Mississippi, appear to occur with a subtidal population of *Callichirus major*, which, like *P. cristata*, has a disjunct distribution pattern along the southeastern coast of the United States, and shows some evidence of morphological divergence between the Atlantic and Gulf populations (R.W. Heard, pers. comm.).

The probable host for the Mexican specimens of *P. cristata* is an undescribed callianassid, near *Callianassa guassutinga*, which is known only from Barra del Tordo, Mexico. However, a number of large, burrowing polychaetes and several large specimens of *Upogebia affinis* (Say) also were taken from the same substrate as the new callianassid, so these cannot be eliminated as potential hosts. The habitat consists primarily of muddy sand partially covered by *Halodule* and, less commonly, *Thalassia* in depths from about 0.3 to 1.0 meters. The collecting site is located just inside of the small embayment that forms the estuarine mouth of the Rio Carrizal, several hundred meters upstream from the point where a small tidal channel breaches a low field of sand dunes to connect the system with the Gulf of Mexico. Salinity was 25 ppt at the time of collection. The Rio Carrizal estuary constitutes a somewhat isolated and atypical feature on this portion of the Mexican coastline, which here tends to lack estuarine embayments and is instead dominated by long stretches of sandy beaches fronting on the open Gulf of Mexico.

Habitats include mouths of estuaries that are subject to
occasional moderate reductions of salinity resulting from runoff.

**DISTRIBUTION.**—Atlantic coast of the southeastern United States, from at least Beaufort, North Carolina, to Miami, Florida; northern Gulf of Mexico, from Horn Island, Mississippi; and southwestern Gulf of Mexico, from Barra del Tordo, mouth of Rio Carrizal, Tamaulipas, Mexico. Intertidal and shallow subtidal to a depth of at least 2 meters.

**Pinnixa gorei, new species**

**FRONTISPIECE, FIGURES 10-12**

**MATERIAL.**—Florida. Fort Pierce Sites: St. Lucie, Atlantic: Sta. FP-82-2, 2 ovigerous females (paratypes, USNM 221643); Sta. FP-82-3, 4 males, 6 females (5 ovigerous) (ovigerous female is holotype, USNM 221640); Sta. FP-83-1, 8 males, 10 females (6 ovigerous) (ovigerous female is holotype, USNM 221644); 1 male, 1 female (paratypes IRCZM 089:06325); Sta. FP-84-1, 2 males, 1 female (paratypes, USNM 221642); Sta. FP-84-4, 1 male, 4 females (paratypes, USNM 221639); 1 male, 1 female (paratypes, USLZ 2951); Sta. FP-85-3, 1 male, 3 females (2 ovigerous) (paratypes, USNM 221641). This locality is the St. Lucie Inlet site of Gore, Scotto, and Becker (1978, fig. 1).

Lake Worth Inlet, Peanut Island: Sta. FP-87-8, 1 male (paratype, IRCZM 089:06391).

Dade County, Key Biscayne, southeastern side of Bear Cut at marina; sand flat exposed at low tide; yabby pump; Sta. RBM Miami-1; R.B. and L.K. Manning, M. Schotte, and R. Lemaitre; 18 Apr 1988; 7 males, 6 females (3 ovigerous), 1 male, 1 female taken with *Callianassa grandimana* (paratypes, USNM 240117). Same locality; Sta. RBM Miami-4; R.B. Manning; 23 May 1988; 3 males, 11 females (6 ovigerous) (paratypes, USNM 240116). Dade County, Virginia Key, southern side of Rickenbacker Causeway at Seaquarium; sand and muddy sand; yabby pump; Sta. RBM Miami-3; R.B. Manning and R. Lemaitre; 22 May 1988; 1 female (paratype, USNM 240118).

**CARIBBEAN SEA.**—Little Cayman Island: 19°41’N, 80°03’W; Oxford University Cayman Expedition; 2 males, 1 ovigerous female (paratypes, BM 1955.10.6.15-17).
FIGURE 11.—*Pinnixa gorei*, new species: *a–d*, chela; *e*, P-4; *f–j*, gonopods; *f,g,i*, sternal face; *h,j*, abdominal face. *a*, female holotype, cb 6.1 mm; *b–d*, male paratype, cb 8.1 mm; *e–h*, male paratype, cb 8.4 mm; *i,j*, male paratype, cb 6.0 mm; all from St. Lucie, Atlantic.
FIGURE 12.—*Pinnixa gorsi*, new species, Little Cayman Island: a, carapace; b, cheliped of male; c, P-4; d, abdomen; e,f, gonopod; g, cheliped of female. a-f, male paratype, cb 9.5 mm; g, ovigerous female paratype, cb 10.2 mm.

**DIAGNOSIS.**—Carapace about 2 (2.0–2.3, mean 2.1) times broader than long in adults (about 1.8 in juveniles), with high, sharp, cardiac crest extending from side to side above posterior margin. No transverse ridge on branchial regions. No sharp carina between orbits, replaced by low boss.

Chelipeds of males and females similar, larger in males. Distal margin of palm almost perpendicular in both sexes, with narrow, rectangular, median tooth; gape above tooth setose in both sexes; tooth relatively higher in males than in females. Dactylus strongly deflexed, with 2 separated teeth in males, larger near midlength, 2 subdistal teeth in females.

Third walking leg (P-4) strongest, merus 2.1 to 2.5 times longer than high (appearing slenderer in figures); posterior half of ventral margin of merus densely setose. Propodus 1.4 to 1.8 times longer than high, with single marginal carina on ventral (opposable) margin. Dactylus not longitudinally ridged.

Male and female abdomens of 7 free somites. First somite of male abdomen trapezoidal, slightly wider than second. Sixth somite with lateral margins concave. Telson longer than sixth somite, apex broadly rounded.

Gonopod as illustrated (Figures 11f, j, 12e, f).

**SIZE.**—Males, cl 2.8 to 4.4 mm, cb 5.6 to 9.5 mm; non-ovigerous females, cl 2.5 to 3.8 mm, cb 4.5 to 7.6 mm; ovigerous females, cl 3.2 to 5.0 mm, cb 7.2 to 10.2 mm.

The largest specimen examined is an ovigerous female, 5.0 × 10.2 mm.

**COLOR IN LIFE.**—Carapace variable in color dorsally, always appearing mottled, usually showing a conspicuous pattern of white, amber, and brown. Median area usually brown or amber, especially on gastric and cardiac regions; lighter areas spotted or variegated with white dominating branchial regions. In dorsal view, chelipeds with spot of white on distal third of merus, large patch of white on outer and upper surface of carpus, and elongate white patch on superior margin of palm.
Walking legs marked by conspicuous white patches and broad, brown bands; isolated white spot often present near midlength of merus, and distinct white patch or band present on distal half of carpus, distal extreme of propodus, and on proximal half of dactylus. Latter pale whitish to translucent. Brown color although a single small male was taken from a clean intertidal sandflat on Peanut Island, Lake Worth.

Remarks.—This new species resembles P. aidae and differs from all other Atlantic species of the Pinnixa cristata Complex in having the branchial regions smooth, not ornamented with a carina. Pinnixa gorei can be distinguished at once from P. aidae by the structure of the opposable margin of the propodus of the fourth pereopod: it is bincarinate in P. aidae, but ornamented with a single carina in P. gorei. The latter species also differs from P. aidae in several features of the chela: the fixed finger is shorter, there are two teeth on each finger, and setae in the gape are restricted to the area above the proximal tooth of the fixed finger.

The occurrence of this species at Little Cayman Island in the Caribbean suggests that it is a tropical species the range of which extends northward at least to southern Florida.

Etymology.—We dedicate this species to our colleague Robert H. Gore, formerly with the Smithsonian Marine Station at Link Port, Fort Pierce, Florida, who made substantial contributions to our knowledge of the biology, development, and systematics of the decapod crustaceans of the Indian River and adjacent area of the Florida east coast.

Biology.—Most specimens of Pinnixa gorei were collected from burrows in a wave-washed tidal pool formed between an emergent sabellarian worm reef (Phragmatopoma lapidosa Kinberg; see Gore, Scotto, and Becker, 1978) and a sand beach. The sand flat ranged in depth to a maximum of about 1 meter at low tide. The flat is formed of clean sand, with some coarse shell hash, and completely lacks vegetation. The flat is inhabited by callianassids, Callianassa grandimana and Callichirus major, the stomatopod Coronis scolopendra, and burrowing polychaete worms. The habitat and associates of the specimen from Little Cayman Island are unknown.

Pinnixa cristata is commonly taken at the St. Lucie Site with both callianassids, but P. gorei was not found to be associated with any burrowing crustacean. At Miami it was taken together with Callianassa grandimana.

In Florida, this species appears to be restricted to a high salinity habitat bathed by longshore currents and surf overwash. Repeated sampling in other habitats within the Indian River lagoon system yielded no additional samples of P. gorei, although a single small male was taken from a clean intertidal sandflat on Peanut Island, Lake Worth.

Ovigerous females were collected in July.

Distribution.—Known only from three localities on the Atlantic coast of Florida (just north of St. Lucie Inlet, just inside the Lake Worth Inlet, and from Bear Cut, Miami) and in the Caribbean from Little Cayman Island in the Caribbean Sca. Intertidal and shallow subtidal to a depth of about 1 m.

Pinnixa patagoniensis Rathbun, 1918

FIGURES 13, 14


Pinnixa cristata.—Coelho, 1970:236.—Coelho and Ramos, 1972:196 [not Pinnixa cristata Rathbun, 1900].

Previous Records.—Brazil. Brazil (Rodrigues, 1971).

State of Amapá: Cabo do Norte (02°13'S, 50°27'W) (Coelho, 1970; Coelho and Ramos, 1972)

State of Rio de Janeiro: 22°05.2'S, 41°00.8'W; 22°57.1'S, 41°00'W (Rodrigues Costa, 1970). State of São Paulo: 10 km north of Itanhaém (24°11'S, 46°47'W) and Mongaguá (24°06'S, 46°37'W) (between Itanhaém and São Vicente) (Righi, 1967). São Vicente (Ilha de São Vicente = 23°57'S, 46°22'W) (Righi, 1967; Fenucci, 1975). Santos (Baía de Santos = 24°00'S, 46°21'W); Enseada de Caraguatatuba (23°40'S, 45°20'W); Santos, frente à Ilha de Urubqueca; Santos, Praia de Bertioga; Ilha de Alcatrazes (24°07'S, 45°42'W), off city of São Sebastião (all Righi, 1967).

Uruguay. Playa La Paloma (Puerto de La Paloma = 34°40'S, 54°09'W) (Fenucci, 1975).


Argentina. San Matías Bay (Golfo San Matías, 41°30'S, 64°15'W), eastern Patagonia; Hassler Expedition; 1 male (paratype of P. patagoniensis, USNM 49248).

Diagnosis.—Carapace about 2.5 (range 2.1 to 2.7) times broader than long in adults, with high, sharp cardiac crest extending from side to side above posterior margin. Branchial regions each crossed by sharp carina, appearing smooth, not tuberculate, mesially extending to orbit, laterally lacking sharp turn toward posterior margin. A carina extending mesially from each orbit, indistinctly mediately.
Chelipeds of males and females dissimilar. Cheliped (P-1) of male stout, distal margin of palm almost perpendicular, with broad, truncate, median tooth; gape more setose above than below tooth, setae not obscuring gape. Fixed finger short, deflexed, with low, subdistal prominence. Dactylus strongly deflexed, unarmcd. Female cheliped smaller, fixed finger longer, fingers extended, dactylus with low triangular tooth near middle.

Third walking leg (P-4) strongest, merus 1.5 to 1.9 times longer than high; merus with short, dense setation on all of posterior surface, especially dense on female. Propodus 1.0 to 1.3 times longer than high, lower (flexor) margin bicarinate. Dactylus with strong longitudinal ridge on anterior and posterior surfaces.

Male and female abdomens of 7 free somites. First somite of male abdomen trapezoidal, wider than second. Abdomen tapering gently from second to fifth somites, not produced laterally at articulations. Sixth somite constricted laterally, margins concave. Telson rounded, as long as but not broader than sixth somite.

Gonopod as illustrated (Figure 14d–i).

SIZE.—Males, cl 3.6 to 5.0 mm, cb 9.8 to 13.1 mm; non-ovigerous females, cl 2.7 to 5.0 mm, cb 6.4 to 13.4 mm; ovigerous females, cl 3.1 to 4.6 mm, cb 6.4 to 12.3 mm.

The largest specimen examined is a female, 5.0 × 13.4 mm. Boschi (1964:55) recorded a male with cl 6 mm and an ovigerous female with cl 5.5 mm. The holotype measures 5.5 × 12.8 mm (Rathbun, 1918).

COLOR IN LIFE.—Not recorded. Boschi (1964:56) stated that preserved animals were “amarillo claro.”

REMARKS.—Pinnixa patagoniensis, which differs from all of the members of the P. cristata Complex in having the branchial ridges extending to the orbit, appears to be the southern counterpart of Pinnixa cristata. Like P. cristata, it occurs over a wide range of latitudes (from 0°N to at least 41°S) and has been taken with a variety of hosts.

Fenucci (1975) synonymized Pinnixa angeloi Righi, 1967 with P. patagoniensis Rathbun, 1918, an action with which we are in complete agreement. The gonopods of these two nominal species appear to us to be identical. We have been able to compare a male paratype from Patagonia with a series of specimens from Brazil, confirming the wide latitudinal range of the species.

BIOLOGY.—Members of this species have been taken in association with several other invertebrates. Righi (1967) reported that his material had been taken with Callrichirius major, and Rodrigues (1971:197) noted “one or two specimens of a crab (Pinnixa angeloi)...are frequently found in the narrow upper part of the burrow” (of Callichirus major). Fenucci (1971, 1975) stated that this species occurs in the burrows of Callianassa and the tubes of Arenicola, and, in 1975, he reported specimens taken with Diopatra, in the burrows of Glossobalanus, and free-living. Boschi (1964) and Fenucci (1975) reported material from the stomach of Mustelus schmitii Springer, 1938 (? = M. canis Mitchill, 1815); one of Boschi’s specimens was from a depth of 110 m to 130 m. Coelho (1970) and Coelho and Ramos (1972) reported material from Brazil taken on muddy bottom in 23 m, and Rodrigues Costa (1970) reported material taken in 12 m and 100 m. Both Righi (1967) and Fenucci (1975) reported on material taken from beaches,
preumably in shallow water near shore.

Boschi (1966, 1976, 1979) characterized this as a warm temperate representative of the Argentine marine fauna.

Ovigerous females have been taken in January (Argentina; Boschi, 1964), May (Brazil; present paper), July, August, and November (Brazil; Rigli, 1967), and December (Brazil; present paper). Boschi (1964) reported that this species carried 2500 to 3000 eggs, and Boschi (1981) gave a brief account of the larvae.

**DISTRIBUTION.—**Atlantic coast of South America, from Cabo do Norte, State of Amapá, Brazil, southward to Golfo San Matias, Argentina. Shallow water to a depth of 130 m.

**Discussion**

By collecting with yabby pumps in intertidal habitats we have taken a wealth of infaunal decapod species, many of which were thought previously to be rare and others of which are new to science (e.g., Felder and Manning, 1986). The more deeply burrowed species in these habitats, and their commensals, tend to escape sampling based upon shoveling and sieving of shallow substrates or the pulling of small dredges by hand or small boat. They are also situated well inshore of depths that can be sampled effectively by large box corers and grabs such as those operated off of research vessels. We feel that this explains in large part why shallow water species of *Pinnixa* and other infaunal decapods have for so long remained undiscovered, and that it justifies an intensified effort to collect the deeper-burrowing infauna in nearshore habitats.

Conspicuous differences in the coloration of live animals initially led us to undertake a systematic re-examination of the *P. cristata* Complex in south Florida, and, to the extent possible, we attempted to evaluate color patterns for other members of the complex in the western Atlantic. As these animals are commensal inhabitants of infaunal burrows, it may seem surprising that color pattern should be developed to any great extent. However, most members of the *P. cristata*
Complex appear to inhabit preferentially the narrowed upper chimney of thalassinid burrows in or near shoreline habitats, where light may at times be intense. Among at least the North American members of this complex (Frontispiece) there is a general tendency for light colored patches or bands (perhaps obliective) to mark the distal extremes of pereopod segments. However, accentuation of this pattern may be conspicuous on the fourth pereopod of P. cristata where the distal third of the propodus is often distinctly and characteristically whitened. On the same article in P. gorei, white is restricted to a more distal extreme, and this difference, along with the brown to amber dorsal patterning of the legs and carapace in P. gorei will readily serve to distinguish animals in the field. However, coloration appears to be much less useful in separation of P. behreae from P. chacei, both of which tend to vary between color morphs that are generally dark or translucent to color morphs that are conspicuously white. The significance of this variation, while not as yet known, does not appear to bear any direct relationship to coloration of substrates, as both color extremes may be taken from the same habitat. While it could relate to depth occupied within the host burrow, and light levels at that depth, this seems unlikely as the color does not change appreciably while animals are subjected to varied lighting conditions and varied backgrounds and held over several days in the laboratory. More likely, the variation relates to some intrinsic factor under endocrine control, perhaps cueed by the molt cycle or sexual maturation and mating. Whatever the case, this pattern of variation is common to both of the two northern Gulf of Mexico species among the North American representatives of the complex, and has contributed to confusion between P. chacei and P. behreae prior to this work.

With completion of this study, makeup of the Pinnixa cristata Complex in the western Atlantic is increased from four to six species. The only additional species known to be a member of this complex is P. felipensis in the eastern Pacific. Of the western Atlantic species, two (P. behreae and P. chacei) appear to be endemic to the Gulf of Mexico, one (P. gorei) is known from southeastern Florida and the Cayman Islands, one (P. cristata), occurs on the Atlantic coast of the southeastern United States and in the Gulf of Mexico as well, and two (P. aidae and P. patagoniensis) are restricted to the Atlantic coast of South America. While it is tempting to make hypotheses regarding origins or dispersal of members in the complex, we must limit such analyses until we have access to more thorough collections. To date, our collecting efforts in intertidal habitats have been concentrated in Florida and the northern Gulf of Mexico, and have been biased to the more accessible localities. Even on populous bathing beaches and in localities thought to be well covered in previous biological surveys, collecting with yabby pumps has produced undescribed species. We thus suspect that much more remains to be discovered about distributions of the P. cristata Complex, particularly in the diverse coastal habitats of Mexico, the Bahamas, the Caribbean, and South America.

In cases where we have been able to rather fully define ranges, the reasons for observed distributions are not readily apparent. For example, we have detected a geographic break in the distribution of two closely related species, both of which appear to be endemic to the Gulf of Mexico and both of which were formerly treated under P. cristata or P. chacei. As herein restricted, ranges of P. chacei and P. behreae break or perhaps narrowly overlap along the Alabama coastline in the northeastern Gulf of Mexico. In coloration, morphology, and habitat, these two species are very similar; furthermore, both appear to inhabit primarily burrows of Callichirus islagrande. While there may be increased tendencies for periodic low salinities in habitats near and immediately west of the Mississippi delta, there is no conspicuous feature in coastal physiography or hydrography that would appear to limit larval dispersal or colonization in this part of the northeastern Gulf and thereby explain the observed distributions of these two species. However, the occurrence of distributional breaks between species pairs in that geographical area has been documented previously for other decapod genera (e.g., Williams and Felder, 1986).

It appears that P. cristata is not common in the northern Gulf of Mexico, even though one of its typical hosts, Callichirus major, is widely distributed there in both intertidal and shallow subtidal habitats. However, the distribution of C. major is disjunct across peninsular Florida, as is the case for a number of decapod species (Williams, 1984:4), and this may well account for the similarly disjunct range of its associate, P. cristata. While C. major and its symbiont P. cristata are dominant forms on intertidal sandy beaches of the southeastern Atlantic coast, they appear to be largely replaced in comparable northern Gulf habitats by Callichirus islagrande and its typical endemic associates, P. chacei and P. behreae. The known occurrence of P. cristata there is instead limited to its association with individuals of a subtidally occurring population of Callichirus major off Mississippi. Where (in a few instances) pinnotherids have been taken with intertidal individuals of C. major in the northern Gulf, the apparent associate has been P. behreae rather than P. cristata.

The slight morphological differences observed between Atlantic coast specimens of P. cristata and those taken from Mississippi and Tamaulipas suggests that these populations are isolated from one another and may be undergoing adaptations to unique hosts or environments. As the specimens from Mexico appear to occur with an undescribed species of Callianassa (near C. guassuina), rather than with the expected hosts, Callichirus major and Callianassa grandiana, this could account for some specialization and divergence. While P. cristata does occur with C. major in at least one northern Gulf locality, it appears that both the pinnotherid and its host exhibit slight phenotypic divergence from Atlantic coast populations; in addition to slight differences that we found between Atlantic and northern Gulf populations of P. cristata, detailed morphological comparisons
between Gulf and Atlantic populations of *Callichirus major* suggest subtle but consistent differences in morphology of eyestalks and selected appendages (R.W. Heard, unpublished observations).

Powers (1977:10) noted that endemism of Pinnotheridae was greater than that known for any other brachyuran family in the Gulf of Mexico, and proposed that specificity for hosts may contribute to this phenomenon. By additional collecting and re-examination of shoreline species, we herein have added to the list of endemic Gulf pinnotherids from the *P. cristata* Complex. However, limited work with other members of the genus *Pinnixa*, particularly from deeper subtidal habitats of the Gulf continental shelf (D.L.F., unpublished data; R.W. Heard, pers. comm.), reveals that many additional species remain to be described in this genus, and suggests that many of those new forms represent yet more endemic species of this highly diversified group of commensals.

From our findings to date in the western Atlantic, diversity of pinnotherid species appears to exceed appreciably that of their thalassinid hosts. In the case of the *P. cristata* Complex, comparison of the North and South American representatives suggests that these pinnotherids and their callianassid hosts have speciated at different rates. *Callichirus major* and *Callianassa grandimana*, among other species, occur off the southern United States and off Brazil as well (Bilhar, 1971; Rodrigues, 1971; Schmitt, 1935). Northern populations of these callianassids have three species of the *Pinnixa cristata* Complex associated with them, *P. behreae*, *P. chacei*, and *P. cristata*; off Brazil these are replaced by two species, *P. aidae* and *P. patagoniensis*. 

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