

WESTERN ATLANTIC SPECIES OF THE
PARAPAGURUS PILOSIMANUS COMPLEX
(ANOMURA: PAGUROIDEA: PARAPAGURIDAE):
DESCRIPTION OF A NEW SPECIES AND
MORPHOLOGICAL VARIATIONS

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A B S T R A C T

A review of the deep-water hermit crabs of the genus *Parapagurus* has shown that 10 of the taxa assigned to this genus, and an additional new species, represent a group of closely related species defined herein as the *P. pilosimanus* complex. Four species of the complex occur in the western Atlantic: *P. pilosimanus*, *P. nudus*, *P. scaber*, and *P. alaminos*, new species. These species are diagnosed or described and morphological variations evaluated and illustrated. Results of this study provide an indication of the range of variations that could be expected in species of the complex in general. Diagnostic characters at the specific level have been found in the branchiostegite, antennal acicle, left cheliped, propodal rasp of the fourth pereopod, uropods, and telson. SEM micrographs of the scales constituting the propodal rasp are included. The right cheliped is shown to be affected by size and sexual dimorphism, and is not useful in distinguishing the species.

Hermit crabs of the genus *Parapagurus* are one of the most conspicuous group of organisms on the continental slope region (200–3,000 m) of practically every major ocean. However, they range from 55 m to nearly 5,000 m depth. Some of the striking symbiotic relationships that many species of *Parapagurus* have developed with members of the Anthozoa are well known. Despite intriguing aspects of their life history, knowledge of the 45 described taxa is poor. The presumed high degree of morphological variability exhibited by these species led carcinologists to divide several taxa into forms, varieties, or subspecies. The problem of understanding variations in the species has been compounded by the paucity of quantitative analyses of character variations in paguroids in general (e.g., Provenzano and Rice, 1966; Lemaitre *et al.*, 1982) that might provide indications of which characters are subject to the greatest variation. *P. pilosimanus* Smith, 1879, the type of the genus, for example, has been divided into a variety of infraspecific taxa as summarized by Alcock (1905) and Gordan (1956), and cited in ecological studies (e.g., Menzies *et al.*, 1973; Wenner and Boesch, 1979; George, 1981).

The presumed broad range of morphological variations exhibited by *P. pilosimanus* led A. Milne Edwards and Bouvier (1892) to conclude that this species actually was a highly variable, cosmopolitan species. Consequently, they considered *P. abyssorum* Henderson, 1888, and *P. a. scaber* Henderson, 1888 (as *P. a. scabra*), to be only variants of *P. pilosimanus*. However, in order to include those representatives of *P. pilosimanus* *sensu lato* that occurred most commonly at great depths (3,650–4,060 m) and which differed significantly from the typical form, they retained Henderson's (1888) *abyssorum* as a variety. This concept of *P. pilosimanus* as a cosmopolitan species has prevailed, as exemplified by de Saint Laurent (1972), who tentatively proposed a division of the species into seven subspecies. De Saint Laurent's subspecific distinctions were based almost exclusively on the variations in the right cheliped, traditionally considered to be of

great diagnostic importance. She did, however, note that there was considerable overlap of character ranges among the subspecies.

A review of the species was undertaken as part of a study on the systematics and ecology of the genus *Parapagurus* (Lemaitre, in preparation). The examination of a large number of specimens revealed that eight or ten of the taxa assigned to the genus, and an additional new species, *P. alaminos*, represent a group of closely related species herein defined as the *P. pilosimanus* complex. Of the taxa assigned to the complex, five that were listed by de Saint Laurent (1972) as subspecies of *P. pilosimanus* are elevated to specific rank; these are: *P. abyssorum*, *P. nudus* (A. Milne Edwards, 1891), *P. scaber* Henderson, 1888, *P. bouvieri* Stebbing, 1910, and *P. benedicti* de Saint Laurent, 1972. Also assigned to the complex are *P. andreui* Macpherson, 1984, and *P. microps* de Saint Laurent, 1972. Tentatively assigned, on the basis of the limited information available from the literature, are *P. latimanus* Henderson, 1888 [as *P. pilosimanus latimanus* (de Saint Laurent, 1972)], and *P. andersoni* Henderson, 1896. In the western Atlantic, this complex is represented by four species: *P. pilosimanus*, *P. nudus*, *P. scaber*, and *P. alaminos*, new species. The species of the complex are characterized by the five following characters: (1) trichobranchiate gills; (2) reduced cornea; (3) antennal peduncles and acicles distinctly overreaching eyestalks; (4) palm of right cheliped rounded laterally and mesially; and (5) males with well-developed paired first and second pleopods (gonopods). The species of the complex have also the deepest bathymetric distributions within the genus, most commonly occurring at about 1,000 m in depth, and the range of at least one species (*P. scaber*) reaches 5,000 m.

From the vast amount of material of the western Atlantic species of the complex available, I have been able to: (1) evaluate the range of morphological variations in these four species; (2) identify reliable characters that can be used for diagnostic purposes; and (3) provide an indication of the ranges of variations that can be expected in species of the complex in general. From the following morphological structures it has been possible to derive a series of characters of diagnostic value at the specific level: (1) branchiostegite; (2) antennal acicle; (3) carpus of left cheliped; (4) propodal rasp of the fourth pereopod; (5) exopod of left uropod; and (6) telson. Particularly noteworthy are the scales of the rasp of the fourth pereopod. SEM examination of the rasp showed that several species in the complex can be characterized by the shape of the scales. Other characters, found to be affected by growth and sexual dimorphism, are of use only if many specimens are available for comparison. Description of the variations of characters derived from the right cheliped has been considered necessary because previous carcinologists have used these characters extensively, assuming that they were of great diagnostic value.

MATERIALS AND METHODS

Primary sources of specimens used in this study have been the collections of the National Museum of Natural History (NMNH); Rosenstiel School of Marine and Atmospheric Science (RSMAS); and Texas A&M University (TAMU). The types of *P. nudus* [Musée Océanographique, Monaco (MO)], *P. pilosimanus* (NMNH), and *P. scaber* [British Museum (Natural History) (BMNH)], have also been examined. Additional material came from the collections of: LGL Ecological Research Associates, Bryan, Texas (LGL); Museum of Comparative Zoology, Harvard University (MCZ); and the Rijksmuseum van Natuurlijke Historie, Leiden (RMNH). A total of 3,174 specimens was examined. Of this total, 325 were *P. nudus*, 2,299 were *P. pilosimanus*, 124 were *P. scaber*, and 426 were *P. alaminos*, new species. The material has been returned to the museum or institution of origin, except for the holotype and some paratypes of *P. alaminos*, new species, which have been deposited in the NMNH. The majority of the specimens were collected during expedition cruises of the following research vessels: *Advance II* (1978), *Alaminos* (1968–1973), *Albatross* (1883–1886), *Atlantis* (1948), H.M.S.

Challenger (1868), *Combat* (1957), *Columbus Iselin* (1972–1978, 1980, 1981), *Eastward* (1967, 1973–1975), *Gerda* (1962–1965, 1967, 1968), *Gilliss* (1972–1976), *John Elliott Pillsbury* (1964, 1966–1971), *l'Hirondelle* (1880), *Michael Sars* (1910), *Oregon I and II* (1951, 1955, 1957–1959, 1962–1964, 1966, 1967, 1969–1971), *Silver Bay* (1958, 1959), *Talisman* (1883), and *Tydeman* (1972, 1977, 1980–1982). For the sake of brevity, full station data are not included under Material Examined, but can be obtained from the information accompanying the specimens. The number of specimens examined of each species is indicated under Material Examined by geographic area. The illustrations represent examples of the overall range of variation of characters. The general morphological terminology used in the text follows that defined by McLaughlin (1974, 1980). The abbreviation SL indicates shield length (to the nearest 0.1 mm), measured from the tip of the rostrum to the midpoint of the posterior margin of the shield. The SEM micrographs were taken at the Smithsonian Institution.

Parapagurus alaminos, new species

Figs. 1E, F; 2F–J; 4E–H, K; 5C, D; 6D–F; 7A, E; 8D, E; 9D, E

Holotype—Male (SL = 10.3 mm), NMNH 228518; type locality: *Alaminos* station 71-A-8-75, 20°05'N, 92°20'W, 1,307 m.

Paratypes.—Western Atlantic: 13 ♂♂, 7 ♀♀, off eastern United States (NMNH, RSMAS); 95 ♂♂, 107 ♀♀, Bahamas Islands and Straits of Florida (NMNH, RSMAS); 93 ♂♂, 71 ♀♀, Gulf of Mexico (LGL, NMNH, RSMAS, TAMU); 15 ♂♂, 7 ♀♀, Caribbean Sea (RSMAS). Eastern Atlantic: 1 ♂, Azores (RMNH); 7 ♂♂, 7 ♀♀, Canary Islands (RMNH); 1 ♂, Cape Verde Islands (RMNH); 2 ♀♀, Gulf of Guinea.

Description—Shield usually as broad as long. Rostrum rounded, slightly overreaching lateral projections, with middorsal ridge. Anterior margin weakly concave. Lateral projections broadly rounded. Anterolateral margins sloping. Posterior margin broadly rounded. Dorsal surface usually well calcified, with longitudinal row of short setae on each side of midline and short transverse row of setae near each posterolateral angle. Anterodistal margin of branchiostegite unarmed.

Ocular peduncles less than half length of shield, ventrobasally inflated, with dorsal longitudinal row of setae. Ocular acicles subtriangular, terminating in strong spine; mesial margins convex, lateral margins sloping; separated by less than basal width of 1 acicle.

Antennular peduncles slender, long, exceeding distal margin of cornea by nearly entire length of penultimate segment, with scattered setae. Ultimate segment nearly twice as long as penultimate. Basal segment with simple to multifid ventromesial distal spine; mesial face unarmed; lateral face with distal subrectangular lobe armed with several small spines, and 1 spine proximally.

Antennal peduncles exceeding distal margin of cornea by nearly entire length of ultimate segment. Flagellum distinctly reaching beyond right cheliped, with numerous setae 1 or 2 flagellar articles in length. Fifth segment with row of setae on lateral and mesial margins. Fourth segment with scattered setae. Third segment with strong ventromesial distal simple or bifid spine. Second segment with strong multifid dorsolateral distal spine; mesial margin with small spine at dorsodistal angle. First segment occasionally with minute tubercle on lateral face distally; ventromesial angle produced, with distal row of small tubercles or spines. Antennal acicle slender, nearly straight in dorsal view; mesial margin setose, armed with 6–12 small spines.

Mandible without distinguishing characters. Maxillule with subrectangular proximal endite; endopod with long distal setae on well-developed internal lobe, external lobe poorly developed. Maxilla with endopod subequal to scaphognathite in distal extension. First maxilliped with endopod slightly exceeding exopod in distal extension. Second maxilliped unarmed. Third maxilliped with mesial spine on basis; ischium with crista dentata developed as series of irregularly sized teeth.

Sternite of third maxilliped with spine on each side of midline. Epistomial spine usually present.

Chelipeds markedly dissimilar, each with carpus and chela covered with moderately dense simple and plumose setae. Right cheliped elongate, strongly influenced in its proportions by size and sexual dimorphism. Angle of inclination of fingers varying approximately from 125–150° (see variations). Each finger terminating in small corneous claw, with numerous tufts of setae on dorsal and ventral surfaces; each cutting edge with irregularly sized, often serrated, calcareous teeth; cutting edge of dactyl with distal row of small corneous spines. Dactyl with irregular rows of tubercles mesially. Fixed finger with irregular row of tubercles laterally. Palm with closely spaced small spines or tubercles on dorsal surface; ventral surface often smooth. Carpus with numerous small tubercles, less numerous on mesial and ventral surfaces. Merus with numerous small tubercles dorsally; mesial and ventral face smooth or with scattered tubercles; ventromesial margin with distal row of sharp or blunt spines. Ischium with 2 or more tubercles on dorsal margin; ventromesial margin sometimes with row of small tubercles. Coxa with ventromesial row of setae, commonly with small tubercles on ventroproximal angle.

Left cheliped slender. Each finger terminating in small corneous claw; dorsal and ventral surface with tufts of setae; cutting edge of dactyl with row of small corneous spines; cutting edge of fixed finger with row of small calcareous teeth. Palm usually smooth except for dorsomesial and dorsolateral row of small spines or tubercles. Carpus and merus subtriangular. Carpus with irregular rows of numerous small spines or tubercles dorsally, less numerous in females (see variations). Merus unarmed, with transverse dorsodistal row of setae, and with or without longitudinal row of setae dorsally. Ischium with scattered small tubercles. Coxa usually with small tubercle on ventroproximal angle.

Ambulatory legs similar from right to left, slender, long, exceeding right cheliped by at least half length of dactyls. Ischium, merus, carpus, and propodus, each with unarmed mesial and lateral faces, and short scattered setae on dorsal margins. Dactyl less than twice as long as propodus, most strongly curved on distal one-third; with dorsodistal and dorsomesial distal row of long setae, and ventromesial row of minute corneous spinules. Propodus unarmed. Carpus with small dorsodistal spine. Ischium and merus unarmed. Coxa of second pereopod with ventromesial row of setae. Anterior lobe of third sternite subsemicircular, setose, armed with small spine.

Fourth pereopod with dactyl subtriangular, shorter than length of propodal rasp, terminating in corneous claw, with ventrolateral row of small corneous spines; propodal rasp with 1–3 rows of ovate scales. Propodal rasp of fifth pereopod occupying subtriangular area extending to about midlength of propodus.

Exopod of left uropod elongate, anterior margin broadly rounded. Telson with shallow, broad sinus separating asymmetrical lobes; terminal margin armed with strong corneous spines.

Male with paired first and second pleopods well developed. Female lacking first pleopods.

Etymology. — This species is named for the Texas A&M research vessel *Alaminos*, in recognition of the extensive work on deep-sea biology conducted aboard her during many cruises.

Distribution. — Western Atlantic: from off the coast of North Carolina to southern Caribbean. Eastern Atlantic: from the Azores and Canary Islands to the Gulf of Guinea. Depth range: 850–3,360 m.

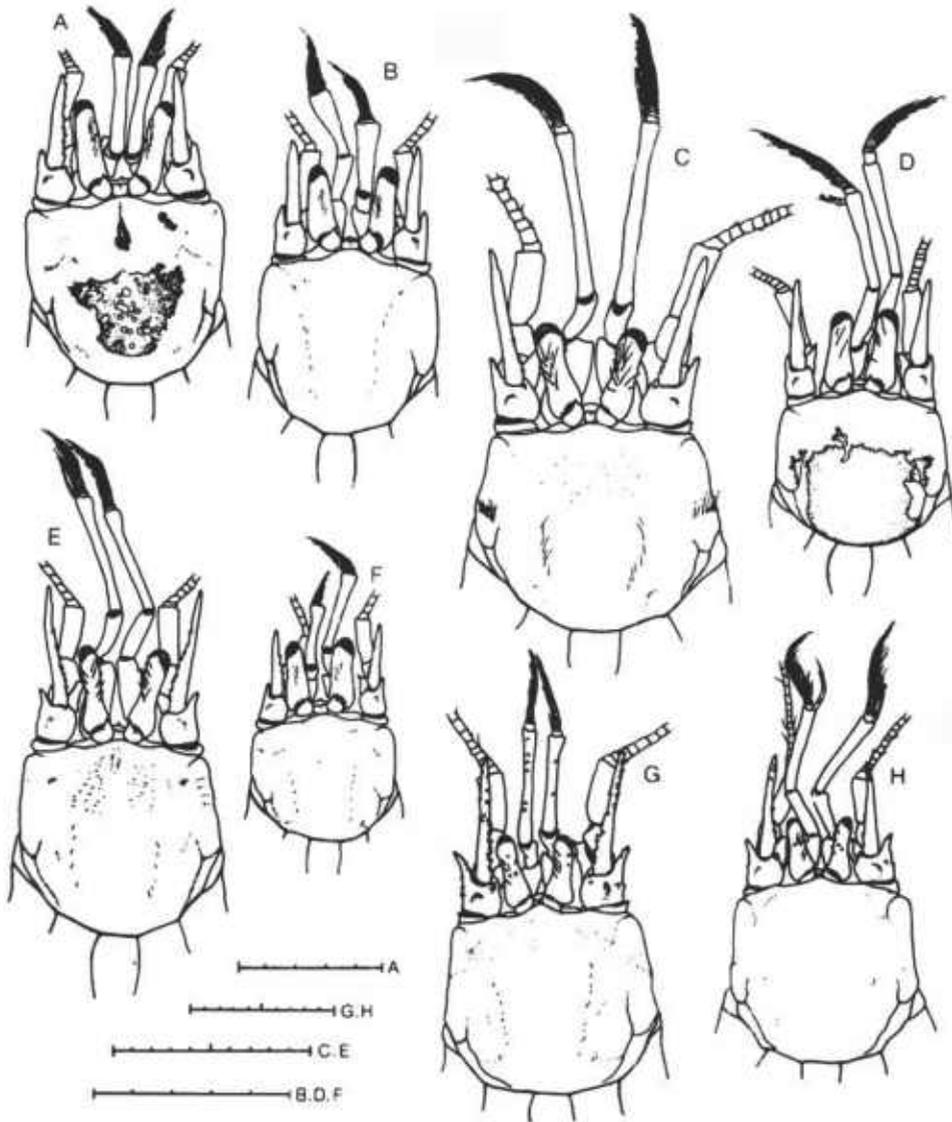


Fig. 1. Shield and cephalic appendages. A, B, *Parapagurus nudus*; C, D, *Parapagurus pilosimanus*; E, F, *Parapagurus alaminos*, new species; G, H, *Parapagurus scaber*. Scales equal 5 mm (A, B, D, F), and 10 mm (C, E, G, H).

Parapagurus pilosimanus Smith, 1879

Figs. 1C, D; 3A-E; 4C, D; 5E, F; 6I, J; 7C, G; 8H; 9F-H

Material Examined.—Western Atlantic: 306 ♂♂, 440 ♀♀, off eastern United States (NMNH, RSMAS); 53 ♂♂, 36 ♀♀, Bahamas Islands and Straits of Florida (NMNH, RSMAS); 591 ♂♂, 347 ♀♀, Gulf of Mexico (LGL, NMNH, TAMU); 242 ♂♂, 204 ♀♀, Caribbean Sea and southwestern Atlantic (RSMAS). Eastern Atlantic: 3 ♂♂, 1 ♀, west of Ireland (RMNH); 1 ♀, Bay of Biscay (RMNH); 24 ♂♂, 32 ♀♀, Azores (NMNH, RMNH); 3 ♂♂, 9 ♀♀, Canary Islands (RMNH); 1 ♂, 1 ♀, Cape Verde Islands (RMNH); 3 ♂♂, 2 ♀♀, Gulf of Guinea (RSMAS).

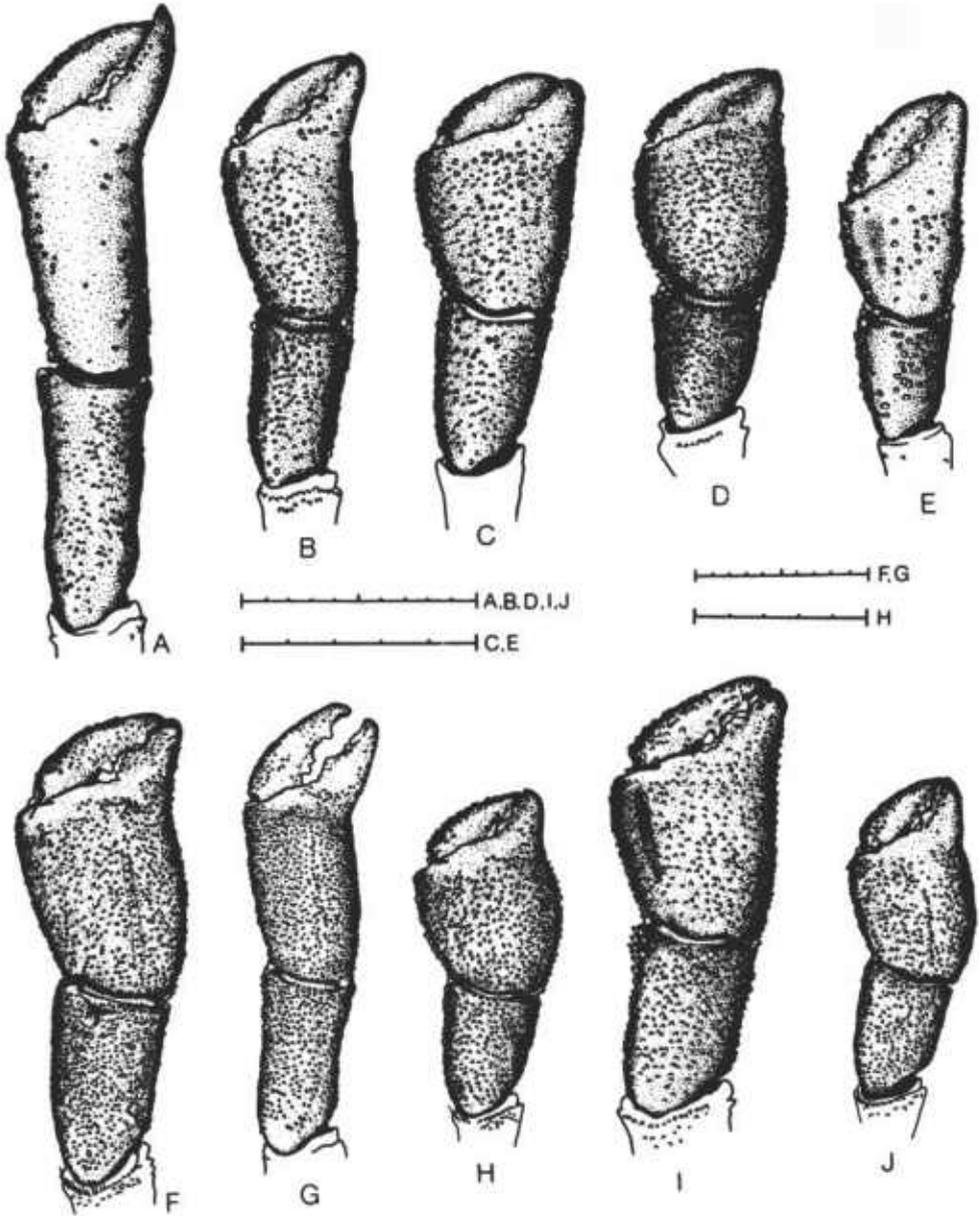


Fig. 2. Carpus and chela of right cheliped (setae omitted). A-E, *Parapagurus nudus*; F-J, *Parapagurus alaminos*, new species. A-C, F-H, males; D, E, I, J, females. Scales equal 5 mm (C, E, H), and 10 mm (A, B, D, F, G, I, J).

Diagnosis.—Anterior margin of branchiostegite unarmed. Antennal acicle unarmed or at most with 1–6 small spines or tubercles on proximal half of mesial margin. Epistomial spine usually absent. Dorsal face of carpus of left cheliped with few small tubercles. Merus, carpus, and propodus of each ambulatory leg unarmed except for dorsodistal spine on carpus. Scales of propodal rasp of fourth

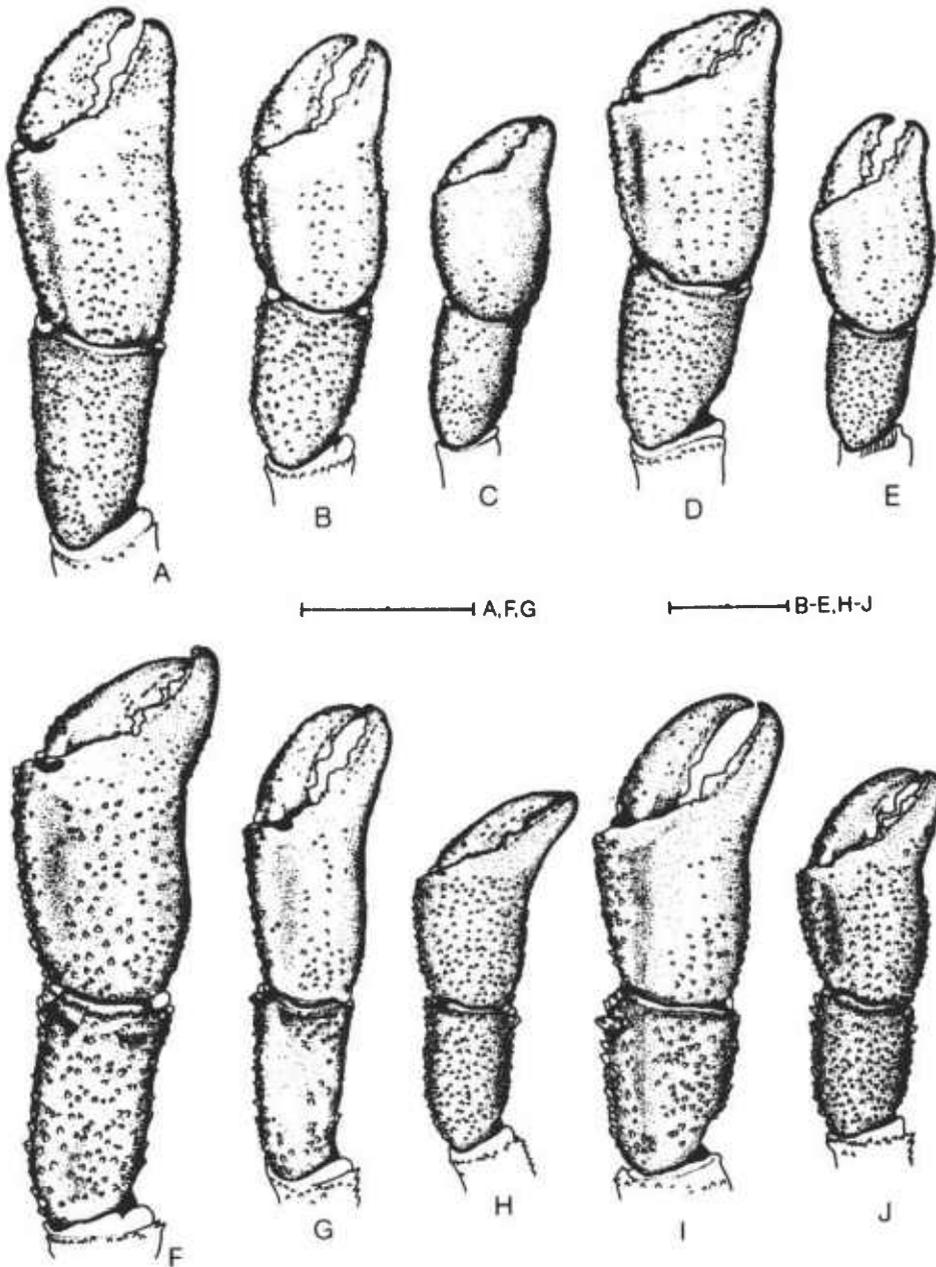


Fig. 3. Carpus and chela of right cheliped (setae omitted). A-E, *Parapagurus pilosimanus*; F-J, *Parapagurus scaber*. A-C, F-H, males; D, E, I, J, females. Scales equal 5 mm (B-E, H-J), and 10 mm (A, F, G).

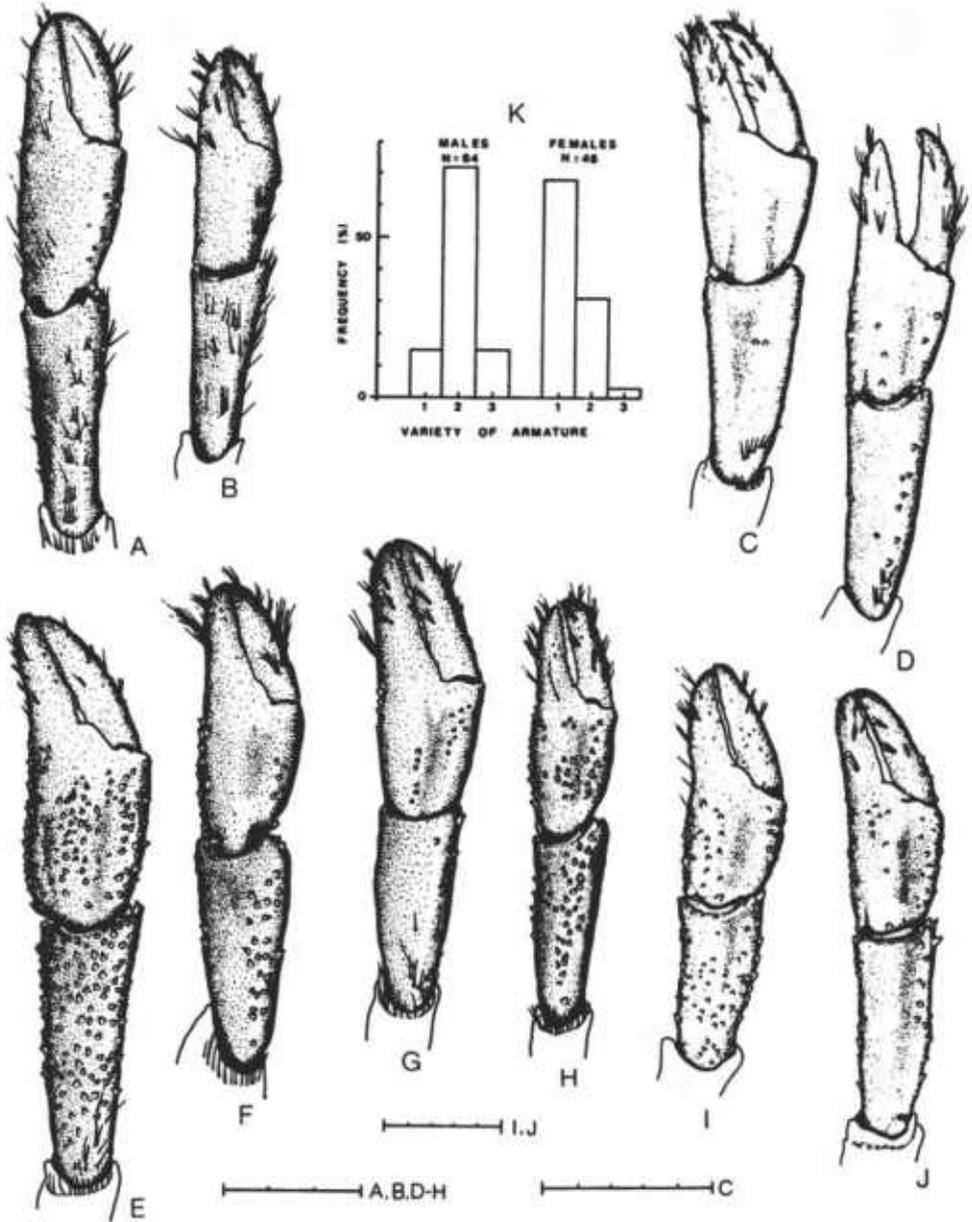


Fig. 4. Variations in armature of left cheliped (A-J), and frequencies of occurrence by sex of varieties of carpal armature (K). A, B, *Parapagurus nudus*; C, D, *Parapagurus pilosimanus*; E-H, K, *Parapagurus alaminos*, new species; I, J, *Parapagurus scaber*. A, E, F, J, males; B-D, G-I, females. Scales equal 3 mm (A, B, D-H), and 5 mm (C, I, J).

pereiopod conical. Terminal margin of telson usually evenly convex, entirely armed with small corneous spines, commonly with very small V-shaped sinus separating generally symmetrical lobes.

Distribution. — Western Atlantic: from off Nova Scotia to Guyana. Eastern Atlantic: from west of Ireland to the Gulf of Guinea. Depth range: 102–3,864 m.

Parapagurus nudus (A. Milne Edwards, 1891)

Figs. 1A, B; 2A–E; 4A, B; 5A, B; 6G, H; 7B, F; 8A–C; 9A, B

Material Examined. — Western Atlantic: 52 ♂♂, 48 ♀♀, off eastern United States (NMNH, RSMAS); 8 ♂♂, 2 ♀♀, Bahamas Islands (NMNH, RSMAS); 10 ♂♂, 8 ♀♀, Gulf of Mexico (NMNH, TAMU); 2 ♂♂, 2 ♀♀, Caribbean Sea and southwestern Atlantic (RSMAS). Eastern Atlantic: 77 ♂♂, 90 ♀♀, Azores (MO, RMNH); 9 ♂♂, 4 ♀♀, Canary Islands (RMNH); 5 ♂♂, 6 ♀♀, Cape Verde Islands (RMNH); 1 ♂, 1 ♀, Gulf of Guinea (RSMAS).

Diagnosis. — Anterior margin of branchiostegite unarmed. Antennal acicle armed mesially with row of spines. Epistomial spine usually present. Dorsal face of carpus of left cheliped unarmed or at most with few small tubercles. Merus, carpus, and propodus of ambulatory legs unarmed except for dorsodistal spine on carpus. Propodal rasp of fourth pereiopod with single distal row of ovate scales. Width of exopod of left uropod frequently more than half exopod length. Telson with terminal margin weakly divided into unequal lobes by shallow, broad sinus; with short corneous spines.

Distribution. — Western Atlantic: from off Nantucket Island to Guyana. Eastern Atlantic: from the Azores and Canary Islands to the Gulf of Guinea. Depth range: 630–3,864 m.

Parapagurus scaber Henderson, 1888

Figs. 1G, H; 3F–J; 4I, J; 5G, H; 6A–C, K, L; 7D, H, I; 8F, G; 9C

Material Examined. — North Atlantic: 39 ♂♂, 56 ♀♀, off northeastern United States (NMNH); 19 ♂♂, 7 ♀♀, mid-North Atlantic (BMNH, NMNH). Eastern Atlantic: 2 ♀♀, Azores (NMNH); 1 ♀, Cape Verde Islands (RMNH).

Diagnosis. — Anterior margin of branchiostegite armed with 1 to several unequal simple or bifid spines. Ocular peduncle and ultimate segment of antennular peduncle commonly armed with small blunt to sharp spines. Antennal acicle armed with spines mesially and often dorsally. Epistomial spine usually absent. Merus, carpus, and propodus of ambulatory legs armed with small spines on mesial and lateral faces. Scales on propodal rasp of fourth pereiopod lanceolate. Telson with terminal margin separated into subequal lobes by shallow sinus; armed with short corneous spines.

Distribution. — North Atlantic, including northeastern coast of United States. Eastern Atlantic: from the Azores to Cape Verde Islands. Depth range: 2,500–5,000 m.

MORPHOLOGICAL VARIATIONS

Shield

Fig. 1

Degree of calcification. — The entire surface is well calcified usually in all four species. However, in *P. nudus* and *P. pilosimanus*, specimens with a shield that is weakly calcified in varying degrees on the posterior half are not unusual. Such weakly calcified regions are irregular in shape, often present as spots, and have a

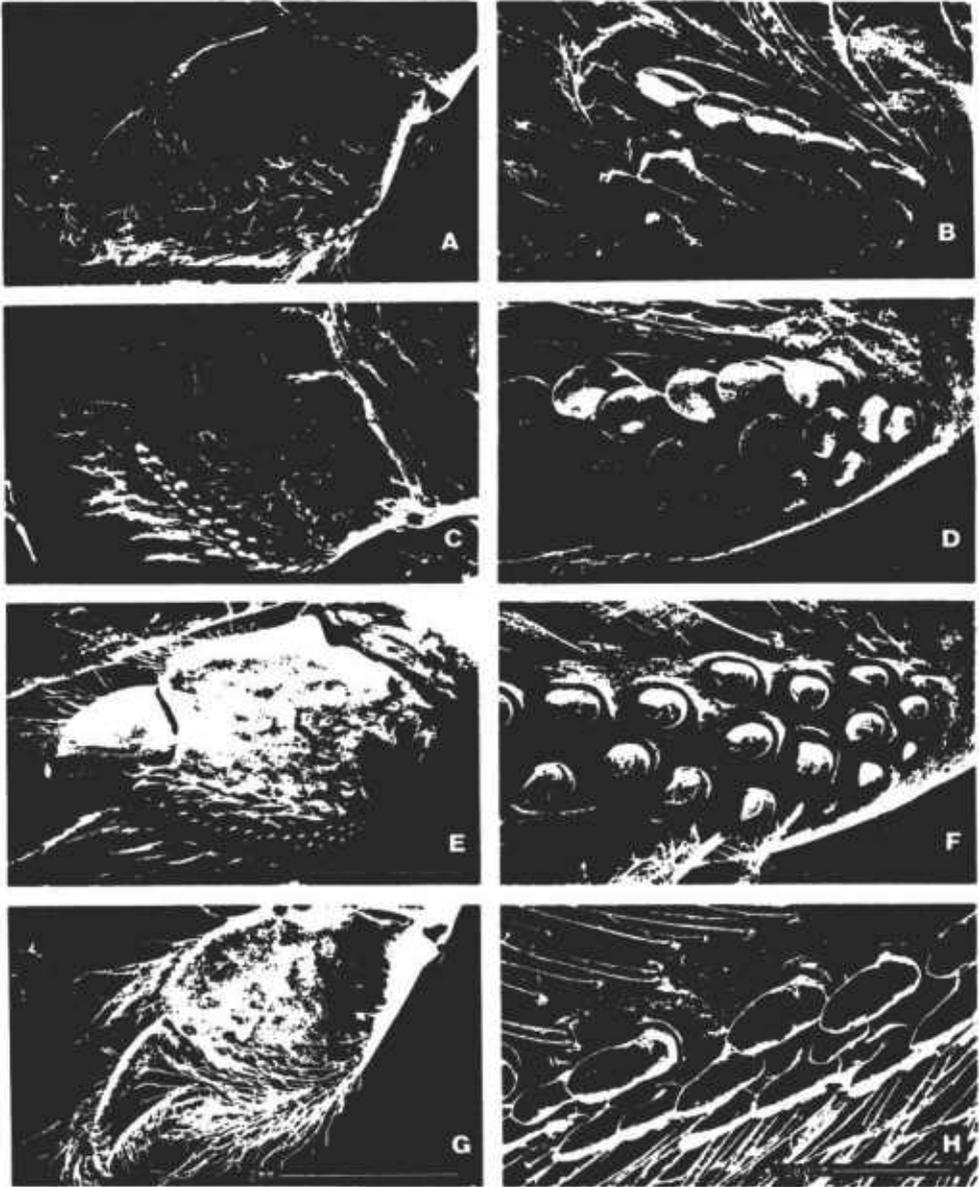


Fig. 5. SEM micrographs of propodus and dactyl (A, C, E, G), and scales of propodal rasp (B, D, F, H) of left fourth pereiopod. A, B, *Parapagurus nudus*; C, D, *Parapagurus alaminos*, new species; E, F, *Parapagurus pilosimanus*; G, H, *Parapagurus scaber*.

more or less transparent appearance (Fig. 1A–D). Calcification can be severely altered during the preservation process; thus the possibility exists that the patterns described are artifacts of preservation. However, various degrees of calcification were found in specimens from the same samples and from a variety of sources. Therefore, such patterns may represent a character that is inherent to the species.

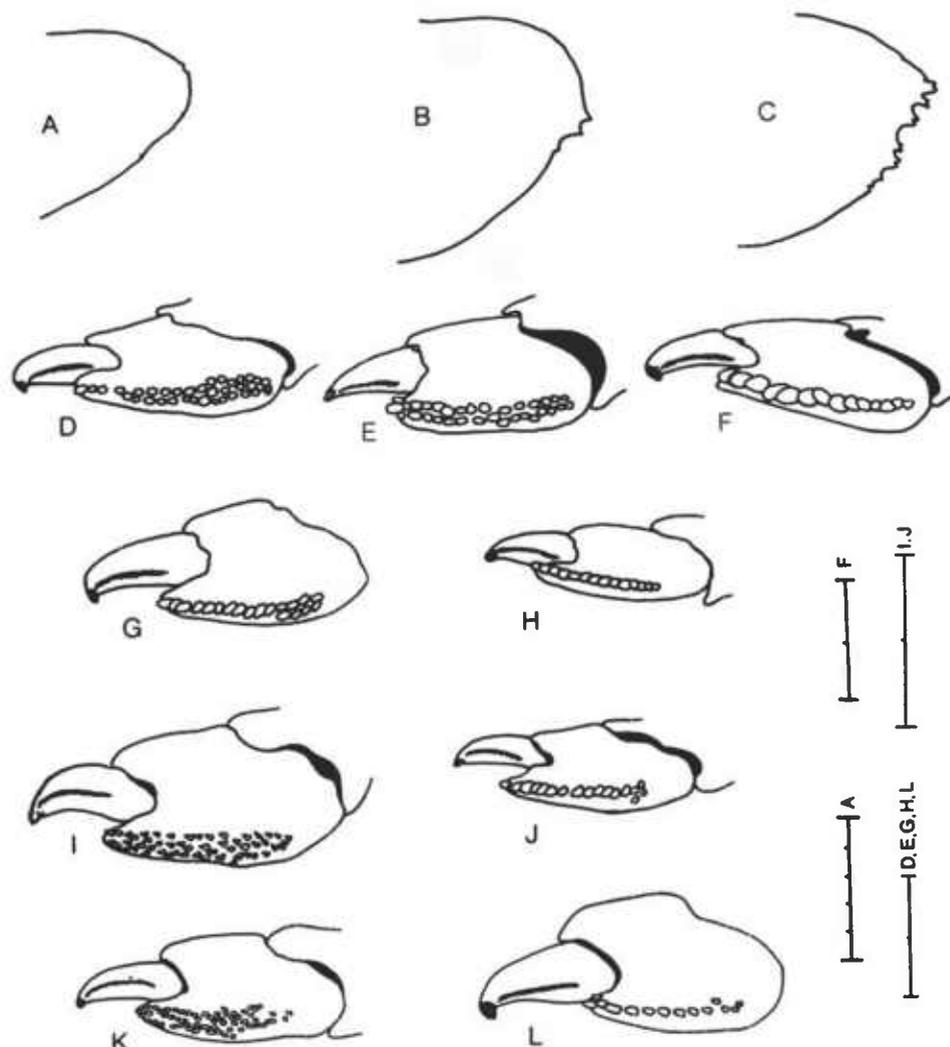


Fig. 6. Anterior margin of branchiostegite (A-C), and lateroventral view of denuded propodus and dactyl of fourth pereiopod (D-L). A-C, K, L, *Parapagurus scaber*, D-F, *Parapagurus alaminos*, new species; G, H, *Parapagurus nudus*; I, J, *Parapagurus pilosimanus*. Scales equal 0.5 mm (F), 1 mm (D, E, G, H, L), 2 mm (I, J), 3 mm (B, C, K), and 5 mm (A).

Branchiostegites Fig. 6A-C

Armature.—The anterior margin of the branchiostegite is unarmed in all species except in *P. scaber*. In this species, the margin is armed with one to numerous single to bifid, unequal spines.

Cephalic Appendages Fig. 1

Shape of ocular peduncle and cornea.—The reduced cornea is a feature common to all species of the complex. The width of the cornea is less than the distal width

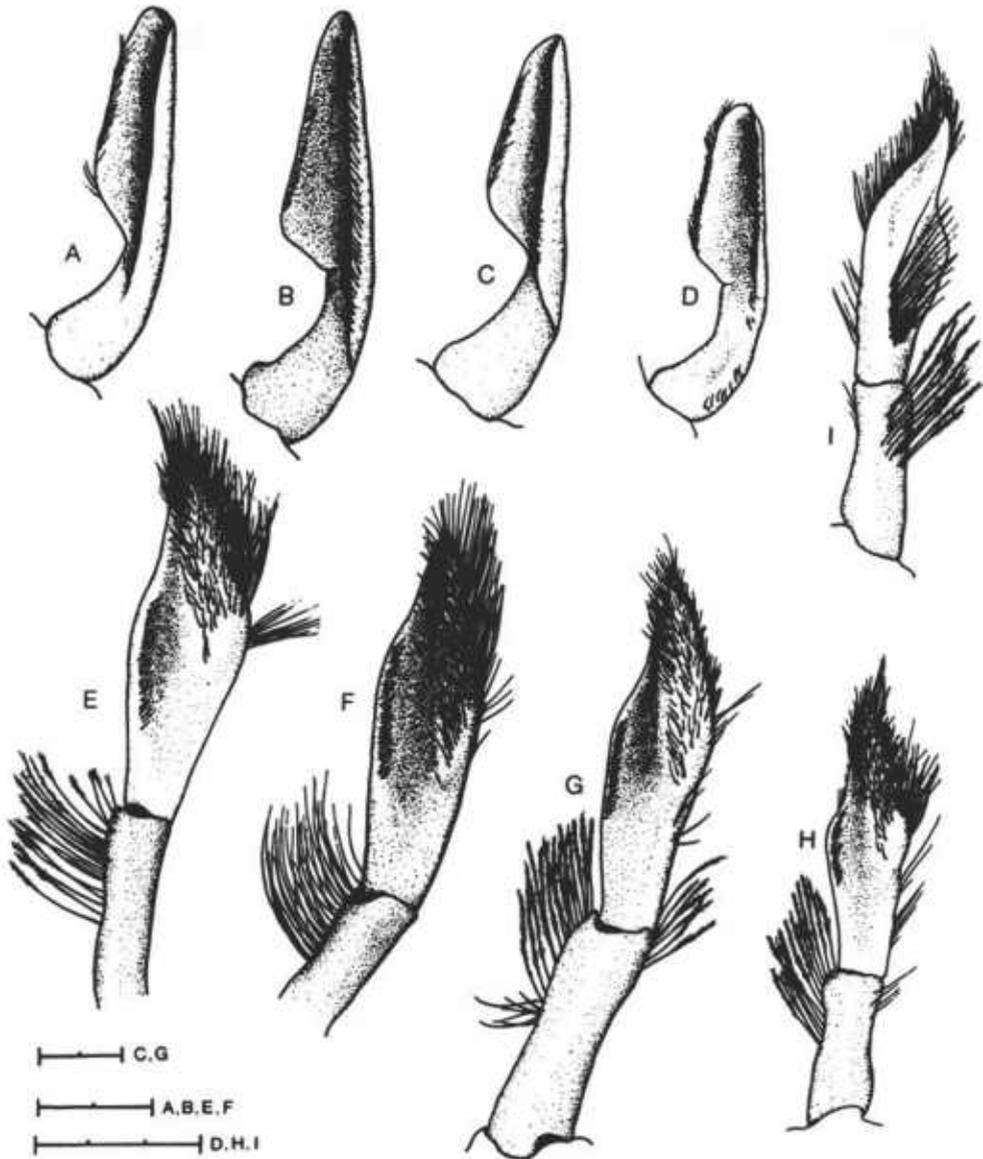


Fig. 7. Male left first (mesial view) and second pleopods (anterior view, E-H; posterior view, I). A, E, *Parapagurus alaminos*, new species; B, F, *Parapagurus nudus*; C, G, *Parapagurus pilosimanus*; D, H, I, *Parapagurus scaber*. Scales equal 1 mm (A-C, E-G), and 3 mm (D, H, I).

of the ocular peduncle. The median part of the peduncle is slightly constricted, and has a row of dorsal setae. The basal part of the peduncle is ventromesially inflated. In *P. scaber*, the peduncle is usually armed dorsally with a few blunt to sharp, small spines. In the other three species the peduncle is unarmed.

Length and armature of antennular segments.—The ultimate segment of the peduncle is normally twice as long as the penultimate segment in all species except *P. scaber*. In that species, the ultimate segment is distinctly less than twice as long

as the penultimate, and may be unarmed, or dorsally armed with 1–4 small, blunt to sharp spines.

Length of antennal peduncle and armature of acicle.—The peduncle and acicle invariably exceed the distal margin of the cornea in all species of the complex. The length by which the peduncle and acicle exceed the cornea, as well as the armature of the acicle, have been found to increase with growth in the four species studied. The acicle is armed mesially with spines in *P. nudus*, *P. scaber*, and *P. alaminos*. In *P. pilosimanus*, the acicle is usually unarmed or bears 1–6 small spines or tubercles on the proximal half of the mesial margin. The variation in the number of spines is greatest in *P. scaber* (range = 5–25; mode = 9; $N = 27$); intermediate in *P. nudus* (range = 0–11; mode = 5; $N = 79$) and *P. alaminos* (range = 4–14; mode = 8; $N = 99$); and smallest in *P. pilosimanus* (range = 0–6; mode = 3; $N = 92$).

Epistomial Spine

Considerable variation in frequency of occurrence of the epistomial spine [="épine interantennulaire," de Saint Laurent (1972: 99)] has been observed. The spine is usually present in *P. nudus* (present: 97.8%; $N = 93$) and *P. alaminos* (present: 97.8%; $N = 362$); whereas the spine is usually absent in *P. pilosimanus* (present: 4.4%; $N = 652$) and *P. scaber* (present: 5.7%; $N = 123$).

Right Cheliped

Figs. 2, 3

Pilosity.—All four species have numerous simple and plumose setae on the segments. The setae are more abundant on the dorsal surface of the carpus and chela, and the density of setation increases with size. The setae do not completely hide the ornamentation of the carpus and chela in *P. nudus*, *P. scaber*, and *P. alaminos*, but they do in large specimens of *P. pilosimanus* (SL > 8.0 mm).

Armature.—Differences in armature exist between the species. However, these differences are difficult to observe without a large number of specimens for comparison. In general, the armature tends to increase with size. Females of *P. nudus*, *P. pilosimanus*, and *P. alaminos* have less armature than males. Females of *P. scaber* have sharper tubercles or spines than males.

Angle of inclination of fingers.—The angle of inclination is herein defined as the external angle that results from the intersection of a line on the longitudinal axis of the palm, with a line from the tip of the fixed finger to the midpoint of the anterior margin of the palm. The range of variation in this angle is smallest in *P. pilosimanus* (140–155°); intermediate in *P. nudus* and *P. alaminos* (125–150°); and largest in *P. scaber* (125–155°). There is considerable interspecific overlap in the range of this angle.

Dimensions of carpus and chela.—The lengths of these two segments, and the ratio palm length/palm width, increase with size much more in males than in females, in all four species.

Left Cheliped

Fig. 4

Carpal armature.—Slight variations were observed in the armature of *P. pilosimanus* and *P. scaber*. The carpus is commonly unarmed in *P. nudus*, although in some cases the dorsal surface may have a few blunt tubercles with tufts of thick setae. The armature was found to be critical in differentiating *P. alaminos* from

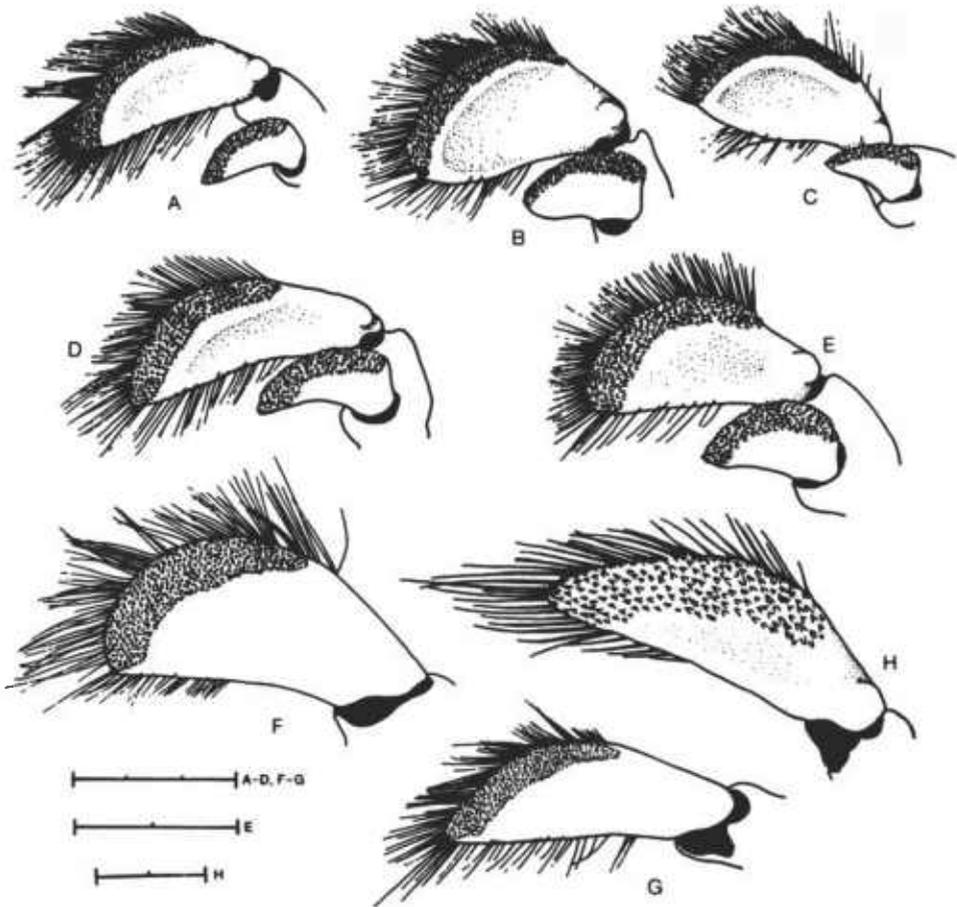


Fig. 8. Exopod and endopod of left uropod. A-C, *Parapagurus nudus*; D, E, *Parapagurus alaminos*, new species. Exopod of left uropod. F, G, *Parapagurus scaber*; H, *Parapagurus pilosimanus*. Scales equal 1 mm (H), 2 mm (E), and 3 mm (A-D, F, G).

P. nudus. Males of *P. alaminos* are immediately distinguished from males of *P. nudus* by the presence, in the former, of numerous small, sharp tubercles on the dorsal surface; whereas in *P. nudus* the carpus is unarmed, or at most bears only a few small tubercles. Females of *P. alaminos* with weakly armed carpi are sometimes difficult to distinguish from females of *P. nudus*. In these cases, other characters must be taken into consideration.

The carpal armature is affected by sexual dimorphism in *P. alaminos*. In order to describe the variation in the carpal armature in this species, three varieties of armature have been defined: (1) few sharp tubercles (Fig. 4G); (2) moderate number of sharp tubercles (Fig. 4F, H); and (3) numerous sharp tubercles (Fig. 4E). In males, the most frequent type of armature is variety 2; variety 3 is commonly found in large specimens (SL > 6.0 mm); and variety 1 is found only in small specimens (SL < 4.0 mm). Females usually exhibit variety 1 in individuals of all sizes; variety 2 is usually found in intermediate to large individuals (SL > 5.5 mm); and variety 3 is rarely found in large females (SL > 6.0 mm). The occurrence of these varieties is summarized by sex in Fig. 4K.

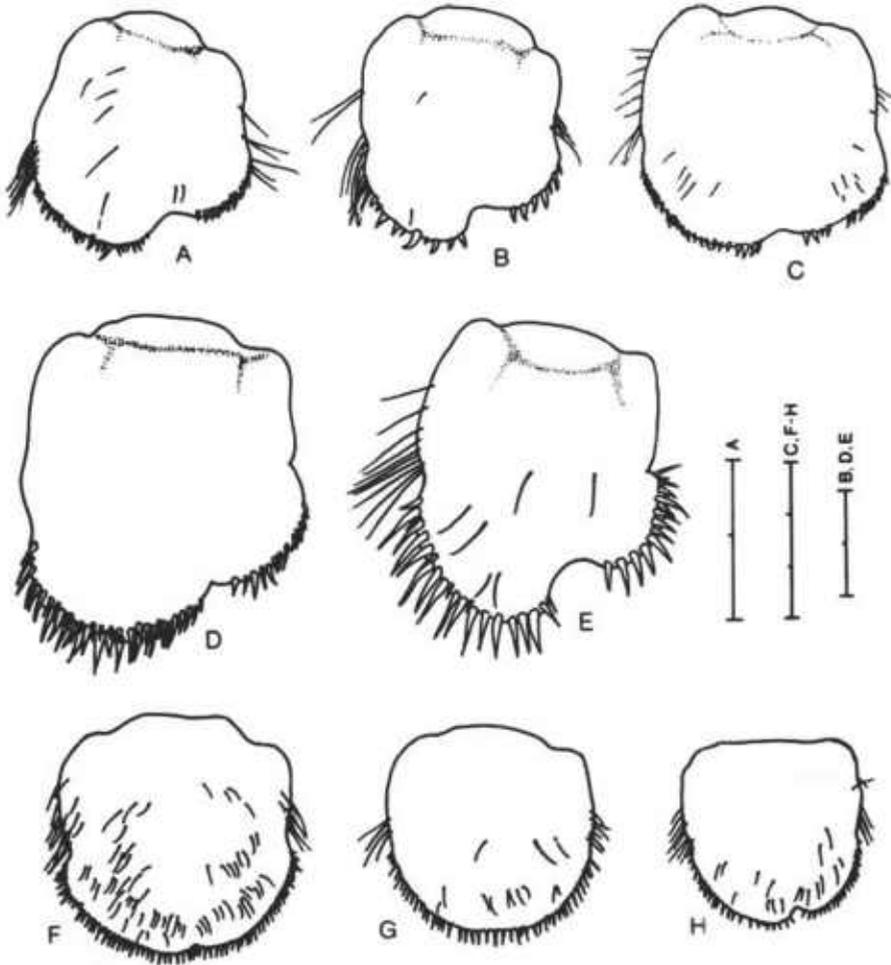


Fig. 9. Telson. A, B, *Parapagurus nudus*; C, *Parapagurus scaber*; D, E, *Parapagurus alaminos*, new species; F-H, *Parapagurus pilosimanus*. Scales equal 1 mm (B, D, E), 2 mm (A), and 3 mm (C, F-H).

Ambulatory Legs (second and third pereiopods)

Length and width of dactyl.—In all four species the length increases considerably with size. The dactyls in *P. nudus* and *P. alaminos* vary from a short, broad type in smaller specimens (SL < 5.0 mm) to a long, slender type in larger specimens. Although changes in the dimensions of the dactyl are similar in both species, the results can be more extreme in *P. alaminos*. Large specimens (SL > 6.0 mm) of *P. alaminos* commonly exhibit longer and more slender dactyls than do *P. nudus* of similar size.

Propodal Rasp of the Fourth Pereiopod Figs. 5, 6D-L

Morphology of the Scales.—The scales are ovate in *P. nudus* and *P. alaminos* (Fig. 5A-D), conical in *P. pilosimanus* (Fig. 5E, F), and lanceolate in *P. scaber*

(Fig. 5G, H). The shape of the scales remains unchanged with size in all species except *P. pilosimanus*. In this species, the scales are ovate in small specimens (SL < 4.0 mm), whereas in larger specimens (SL > 4.0 mm) the scales are invariably conical.

Number of rows of scales.—The maximum number of rows of scales on the distal two-thirds of the rasp varies as follows: 1–3 rows in *P. pilosimanus* and *P. scaber*; 1 or 2 rows in *P. alaminos*; and invariably one row in *P. nudus*. The number of distal rows of scales can often be used in differentiating *P. nudus* from *P. alaminos*. The number of rows of scales on the proximal one-third of the rasp is usually greater than the number of distal rows.

Pleopods

Fig. 7

The first and/or second pleopods are modified as gonopods in males. The morphology is similar in all species of the complex. The first gonopod is unsegmented and has an elongate subcylindrical or subconical distal lobe with a row of setae on both the anteromesial and posteromesial margins. The second gonopod is divided into two segments: (1) a distal segment terminating in an acute tip; and (2) a slender basal segment. The distal segment has an inwardly twisted distomesial margin with numerous setae, and a lateral row of short bristles medially. The posterior face of the distal segment is usually naked, or has scattered setae; however, in *P. scaber*, a longitudinal row of long, plumose setae is frequently present (Fig. 7I). A vestigial exopod rarely is present on the basal segment. The unpaired third-fifth left pleopods have a short exopod.

Females typically lack a first pair of pleopods; however, a pair of vestigial or poorly developed pleopods is frequently found in *P. pilosimanus* and *P. scaber*. These pleopods consist of a short unsegmented bud on each side of the abdomen. The left unpaired second-fourth pleopods have crossed rami. The fifth pleopod is shorter than the second-fourth pleopods, the rami are not crossed, and the exopod is much shorter than the endopod.

Uropods

Fig. 8

Length/width ratio of left exopod.—Although considerable interspecific overlap occurs in the range of variation of the left exopod, certain generalizations can be made about the exopod that can be of use in characterizing the four species. The ratio of the length/width of the exopod in *P. nudus* is usually smaller than in the other three species. The width of the exopod in this species is commonly half or more its length. The broad type of exopod shown in Fig. 8B is found only in this species, and can be of use in separating *P. nudus* from *P. alaminos*.

Telson

Fig. 9

Shape of terminal margins.—The terminal margins of the telson are divided into unequal lobes by a shallow, unarmed sinus in *P. nudus*, *P. scaber*, and *P. alaminos*. In *P. pilosimanus* (except in small specimens, SL < 4.0 mm), the terminal margin is evenly convex, entirely armed, with the lobes separated by a small V-shaped, armed sinus.

DISCUSSION

The systematic confusion that has long existed in the taxa of the *P. pilosimanus* complex has largely resulted from the use of inadequate diagnostic characters, and a misunderstanding of the amount of morphological variation exhibited by the species. Of the characters discussed above, those derived from the branchios-tegite, antennal acicle, left cheliped, propodal rasp of the fourth pereopod, exopod of left uropod, and telson, have been found to be critical in distinguishing the western Atlantic species. Of these characters, only the armature of the antennal acicle has previously been used in diagnosis of the taxa of the complex (Macpherson, 1984).

As previously stated, taxonomic characters derived from the right cheliped had been the most used in distinguishing taxa of the complex. Definitions of the various infraspecific taxa that had been proposed for *P. pilosimanus* were based almost exclusively on the presumed morphological differences in this cheliped (A. Milne Edwards and Bouvier, 1892; Alcock, 1901; de Saint Laurent, 1972). I have shown that the dimensions and armature of the right cheliped are affected by size and sexual dimorphism in a similar way in at least four species of the complex. As a result there is considerable interspecific overlap in the range of morphological variations of the cheliped, thus making characters derived from this appendage virtually useless at the specific level.

Although morphological variations within species in taxa of the complex have previously been assumed to be extremely high, from the evidence presented here it is apparent that this type of variation is not as great as had been believed. Compared to the intraspecific variations described for other paguroids (e.g., Provenzano and Rice, 1966; McLaughlin and Provenzano, 1974; Lemaître *et al.*, 1982; Forest, 1984; McLaughlin and Haig, 1984), the range of variations in the four species studied is similar, or in some cases less, than in other hermit crab groups. As is the case in many paguroids, there is a high degree of interspecific overlap of character ranges in species of the complex. It is only the unusual species that can easily be separated by a single character. Rather, a combination of diagnostic characters must be used in distinguishing the various species.

One of the most significant findings of this investigation has been recognition of the diagnostic significance of the scales of the rasp of the fourth pereopod. The shape of the scales appears to be correlated with the type of shelter used. The two species that use gastropod shells (*P. nudus* and *P. alaminos*) have ovate scales, whereas the two species that live in symbiosis with zoanthid polyps (*P. pilosimanus* and *P. scaber*) have conical or lanceolate scales. The interior walls of the shelters in the latter two species are formed by the polyps and are not calcareous. Since the rasp of the fourth pereopod is used in entering and exiting of the shelter (Dunham, 1983), it is logical to conclude that conical or lanceolate scales have evolved as an adaptation to facilitate the grasping of the interior walls. Conical scales are also present in two eastern Atlantic species of the complex, *P. andreui* and *P. bouvieri*, that also live symbiotically with zoanthid polyps.

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