REVISION OF THE GENUS *PARAPAGURUS* (ANOMURA: PAGUROIDEA: PARAPAGURIDAE), INCLUDING REDESCRIPTIONS OF THE WESTERN ATLANTIC SPECIES

by

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Key words: Deep-water hermit crabs; *Parapagurus*; *Strobopagurus*; *Sympagurus*; systematic revision; new genus; new species; morphological variation; symbiotic associations.

As a result of a revision of the genus *Parapagurus* Smith, three genera are proposed: *Parapagurus* sensu stricto, *Strobopagurus* gen. nov., and *Sympagurus* Smith *reinstated.* Diagnoses of the three genera are given, and a number of structures are described. A key to aid in the identification of the genera of the family is presented. All taxa heretofore assigned to *Parapagurus* are reassigned. Four species of *Parapagurus* and six of *Sympagurus* occur in the western Atlantic, including a new species, *Sympagurus acinops*. All western Atlantic species are redescribed. *Parapagurus abyssorum* (Filhol) is a senior homonym of the eastern Pacific *Parapagurus abyssorum* Henderson, and a new name, *Parapagurus holthuisi*, is given to Henderson's taxon. The subspecies of *Parapagurus pilosimanus* Smith and *Sympagurus bicristatus* (A. Milne Edwards) are elevated to specific rank. *Sympagurus arcuatus* A. Milne Edwards & Bouvier, is a junior synonym of *Sympagurus gracilis* (Henderson). The treatment of each species includes a synonymy, illustrations, comments on symbiotic associations, and a distributional map. Keys to aid in the identification of the western Atlantic species are presented. The morphological variation of the western Atlantic species of *Sympagurus* is described.

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INTRODUCTION

Hermit crabs of the genus *Parapagurus* form one of the most conspicuous groups of organisms on the continental slope (200-3000 m) of every major ocean. However, they range from depths of 55 m to 5000 m. Species of *Parapagurus* have frequently been depicted as typical inhabitants of the deep-sea (e.g., Filhol, 1885a,b; Bruun, 1956; Menzies et al., 1973). Several species have attracted the attention of zoologists since early times because of the striking symbiotic relationship that they have developed with members of the Anthozoa (actinians and zoanthids). Despite the ubiquity and intriguing aspects of the biology of these crabs, knowledge of most of the taxa is poor.

As now constituted, *Parapagurus* contains the majority of the species of the family Parapaguridae. Three monotypic genera are also included in this family and are represented by the highly specialized forms *Probeebei mirabilis* Boone, *Tylaspis anomala* Henderson, and *Typhlopagurus foresti* De Saint Laurent. The interpretation of species of *Parapagurus* has long presented a problem for carcinologists who have considered that species of this genus exhibit a broad range of morphological variation. For example, in the case of *Parapagurus pilosimanus*, the type of the genus, this presumed variability led investigators to describe a number of infraspecific taxa. Many of these, however, were inadequately described, and as a result their taxonomic status has remained confused and their relationships obscure.

The taxonomic confusion that has existed among taxa of *Parapagurus* can be attributed, at least in part, to the use of inadequate diagnostic characters. A survey of the characters used in the diagnoses of the various species and subspecies clearly indicates the tendency to assign great diagnostic importance to characters derived from the right cheliped. Recent studies, however, have shown that the right cheliped in several paguroid genera is greatly influenced by growth, sexual dimorphism, type of shelter used, and environmental conditions (e.g., McLaughlin, 1974; Lemaitre et al., 1982; McLaughlin & Haig, 1984; Blackstone, 1985). Within species of *Parapagurus*, the right cheliped has also been shown to be similarly affected (Lemaitre, 1986), and, as a result, considerable interspecific, as well as intraspecific, overlap occurs in the range

of characters. The fact that many *Parapagurus* taxa have been defined primarily by characters of this appendage makes specific and/or subspecific interpretation difficult or impossible.

The initial objective of this investigation was to review the genus *Parapagurus* and to redescribe the western Atlantic species. As previously defined, the genus contained a morphologically diverse group of species and subspecies adapted to a variety of ecological conditions and shelters. A review of the taxa on a world-wide basis quickly showed the heterogeneity of *Parapagurus*, and the need for its revision. As a result of this revision, two groups of species have been found to be sufficiently distinct from all others to warrant assignment to separate genera. The genus *Parapagurus* is herein restricted to one of these groups, formed by the eleven species of the *P. pilosimanus* complex (cf. Lemaitre, 1986), four of which occur in the western Atlantic. A second group is formed by three species assigned to *Strobopagurus* gen. nov., of which none have been found in the western Atlantic. The genus *Sympagurus* is reinstated and broadly defined to include the remaining taxa (twenty-nine species and three subspecies), although it is recognized that they still represent a morphologically diverse assemblage. Six species of *Sympagurus* occur in the western Atlantic.

During the course of this study two new species have been discovered, *Parapagurus alaminos* Lemaitre, 1986, and *Sympagurus acinops* spec. nov., and a number of taxonomic problems have been clarified. *Parapagurus abyssorum* Henderson, has been found to be a junior homonym of the Atlantic *Parapagurus abyssorum* (Filhol); therefore a new name, *P. holthuisi*, is given to Henderson's taxon. *P. scaber* Henderson, is a junior synomym of Filhol's *P. abyssorum* . The subspecies proposed by De Saint Laurent (1972) for *P. pilosimanus* Smith, and *Sympagurus bicristatus* (A. Milne Edwards), are elevated to specific rank. The distribution of *Parapagurus pilosimanus* has been found to be restricted to the Atlantic. In addition, *Sympagurus arcuatus* A. Milne Edwards & Bouvier is a junior synonym of *S. gracilis* (Henderson).

The availability of a vast amount of material of several western Atlantic species has been extremely useful to the present study. Detailed examination of this material has made it possible to: 1. evaluate the range of morphological variation in these species, 2. identify reliable diagnostic characters, and 3. provide an indication of the ranges of variation that can be generally expected in species of *Parapagurus* and *Sympagurus*. The morphological variation observed in the four species of *Parapagurus* were described by Lemaitre (1986); therefore, only the variation in the species of *Sympagurus* is included here.

The inclusion of a section entitled "Morphological Considerations" is necessary to clarify terminology and to describe several unique or diagnostically

important structures. The "Systematic Account" includes: 1. a key to the genera of the family Parapaguridae, 2. diagnoses of *Parapagurus*, *Strobopagurus* gen. nov., and *Sympagurus*, 3. keys to aid in the identification of the ten western Atlantic species, and 4. a complete synonymy of each of these. Because of the inadequacy of previous descriptions, it has been necessary to include redescriptions of the western Atlantic species [except for *Parapagurus alaminos*, recently described by Lemaitre (1986), for which only a diagnosis is given]. Accompanying the redescriptions are detailed illustrations of the species, distributional maps, and brief notes on the symbiotic associations.

HISTORICAL RESUMÉ

Smith (1879) described *Parapagurus* on the basis of the trichobranchiae of *P. pilosimanus* Smith. Subsequently (1882), he considered the trichobranchiae of this species to be unique among hermit crabs and proposed the monotypic family Parapaguridae for this genus. Shortly thereafter, Smith (1883) described another monotypic genus, *Sympagurus*, for *Sympagurus pictus* Smith. He noted that *Sympagurus* was very similar to *Parapagurus*, except that the former had phyllobranchiae. In his description of *Sympagurus*, and in subsequent reports of *S.* pictus, Smith did not indicate the familial placement of *Sympagurus* (cf. Smith, 1883, 1884, 1886). Trichobranchiae were later found to be present in other paguroid genera and Henderson (1888) proposed two divisions for paguroids based on branchial structure: Laminibranchiata for those forms with phyllobranchiae (Coenobitoidae and Paguridae), and Fibribranchiata for those forms with trichobranchiae. Henderson expanded the Parapaguridae to include all genera with trichobranchiae, i.e. *Parapagurus*, *Pagurodes* Henderson, *Paguropsis* Henderson, and *Pylocheles* A. Milne Edwards. Henderson's parapagurids were united only by gill structure and by their deep-water habitat.

Henderson's use of gill structure and arrangement as a primary character for systematic grouping was criticized by Bouvier (1891a) who cited examples of several closely related genera with different types of gills. He suggested that in paguroids the change from trichobranchiae to phyllobranchiae had occurred progressively and independently in various groups. In Bouvier's view, it was not natural to separate *Parapagurus* from *Sympagurus* based on the type of branchiae. Despite Bouvier's criticism, Ortmann (1892) continued to use the Parapaguridae for those forms with trichobranchiae, and added another genus, *Cheiroplatea* Bate, to the family. Milne Edwards & Bouvier (1893, and subsequent publications), disagreed with the concepts of the family Para-

paguridae as defined by Smith (1882) and Henderson (1888), and placed *Parapagurus*, as well as *Sympagurus*, in the family Paguridae. Although at that time carcinologists agreed on the lack of significance of branchial structure at the familial level, the use of branchial structure at the generic level to separate *Parapagurus* from *Sympagurus* was continued (Milne Edwards & Bouvier, 1893, 1894a, 1897, 1899, 1900; Alcock, 1901, 1905; Bouvier, 1922, 1940; Melin, 1939; Thompson, 1943). However, to Balss (1912), the separation of the two genera seemed unsustainable and he formally placed *Sympagurus* in synonymy with *Parapagurus*. Since then, most carcinologists (e.g., Terao, 1913; Forest, 1955; De Saint Laurent, 1972) have accepted this latter arrangement, except Edmondson (1925), who described a species under *Sympagurus*. A specimen in poor condition reported by Rathbun (1919) as "*Sympagurus* sp." is not a parapagurid and represents an undetermined species of *Iridopagurus* De Saint Laurent-Dechancé.

The family Parapaguridae was reinstated and redefined by De Saint Laurent (1972) based on larval and adult morphology. In addition to *Parapagurus* (including *Sympagurus*), De Saint Laurent included three monotypic genera in the family, *Tylaspis* Henderson, *Probeebei* Boone, and a new genus described as *Typhlopagurus*. Previously, *Tylaspis* had been placed in the Paguridae (Henderson, 1888). *Probeebei* was originally described as a primitive macruran by Boone (1926a,b) for which she proposed the family Probeebeidae. Subsequently, in his redescription of *Probeebei mirabilis*, Wolff (1961a,b) showed that the species was really a hermit crab and placed it in the Paguridae.

In her reinstatement of the family Parapaguridae, De Saint Laurent (1972) broadly defined the genus *Parapagurus* and included twenty-eight species and thirteen subspecies. Since that time, five new species have been described (De Saint Laurent, 1973; Kensley, 1973; Macpherson, 1983b, 1984; Lemaitre, 1986).

MATERIALS AND METHODS

Primary sources of specimens and types used in this study have been the collections of: National Museum of Natural History, Washington, D. C. (USNM); Rosenstiel School of Marine and Atmospheric Science, University of Miami (UMML); Texas A&M University, College Station, Texas (TAMU); Rijskmuseum van Natuurlijke Historie, Leiden (RMNH); British Museum (Natural History), London (BM); Museum of Comparative Zoology, Harvard University (MCZ); Musée Océanographique, Monaco (MO); and Museum National d'Histoire Naturelle, Paris (MNHNP). Additional

material was provided by the following museums and institutions: Instituto de Investigaciones Pesqueras de Barcelona (IIPB); LGL Ecological Research Associates, Bryan, Texas; and South African Museum, Capetown (SAM). A total of 4513 specimens was examined, part of which was used by Lemaitre (1986). The material used by Lemaitre is not listed here. All specimens have been returned to the museums or institutions of origin. For the sake of brevity, full station data are not included under "Material examined", but can be obtained from the "Appendix" or the information accompanying the specimens. The number of specimens examined of each species is indicated by geographic area, from north to south, and the place of deposition indicated in parenthesis. 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.

MORPHOLOGICAL CONSIDERATIONS

In general, the terminology for morphological structures of species of *Parapagurus*, *Strobopagurus* gen. nov., and *Sympagurus*, conforms with that of other paguroids as described by McLaughlin (1974, 1980). However, several unique or diagnostically important structures that have not been adequately described previously, require clarification.

The presence of two median unpaired spines on the epistomial region (fig. 1A) in species of the Parapaguridae is unique among the Paguroidea [except for *Parapylocheles scorpio* Alcock, (De Saint Laurent, 1972)]. One of these spines, located on the center of the epistome, is not always present. De Saint Laurent (1972: 98) called this spine the "épine interantennulaire"; however, the term "epistomial spine" is more indicative of its location and this term is adopted here. A labral spine is formed by an anterior extension of the labrum and is invariably present in all parapagurids. In some species the labrum is separated from the epistome by a suture, whereas in others the labrum is fused to the epistome.

Four types of branchiae are present in the species: 1. trichobranchiae, a series of four filamentous, often flattened branches arranged along the axis (fig. 2L,M), 2. phyllobranchiae, a series of paired, flattened branches along the axis (fig. 2H), 3. intermediate branchiae between types 1 and 2, and consisting of series of paired flattened branches distally divided (fig. 2I,J,K), and 4. vestigial branchiae, represented by small buds (fig. 2G).

The second abdominal somite and the pleopods are diagnostically important. The left pleuron of the second abdominal somite is unique in that it terminates ventrally in a small subtriangular lobe (fig. 1B). The male first

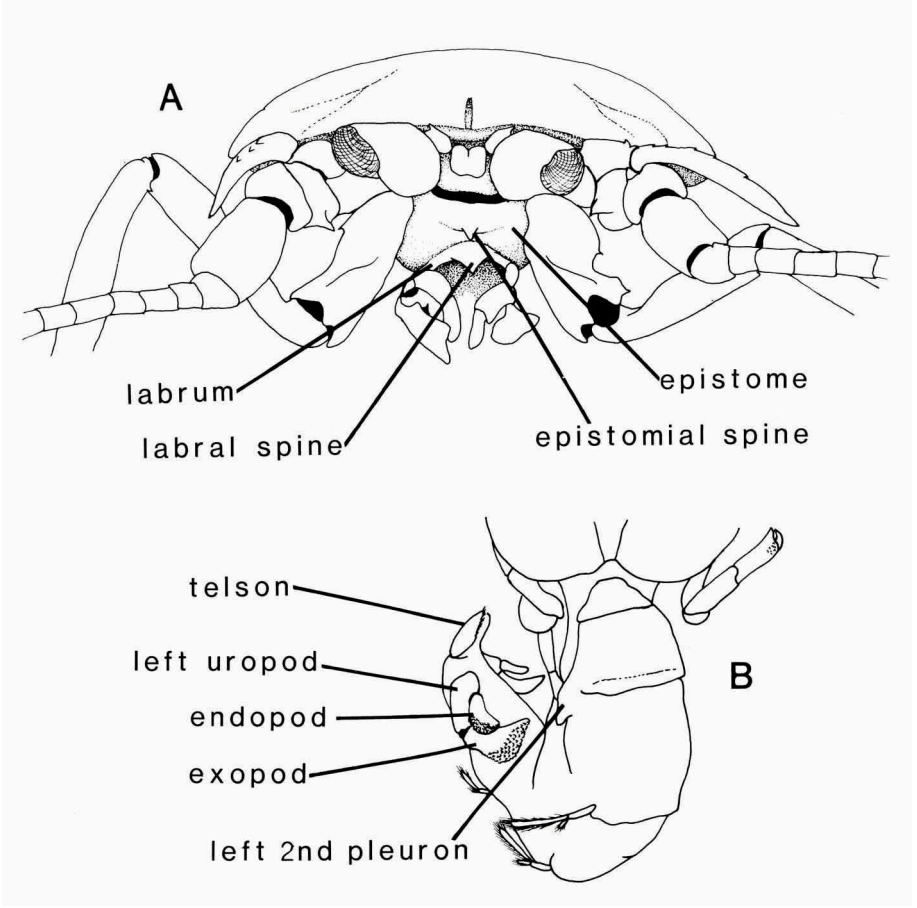

Fig 1, diagrammatic parapagurid, depicting terminology used in text. A, shield and cephalic appendages (frontal view); B, male abdomen (dorsal view).

pleopods are unsegmented, consisting of a basal, slender portion, and a distal lobe that varies in shape (fig. 2A,D). A short exopod on the first pleopod has been reported only in one species (*Sympagurus sinensis* De Saint Laurent, 1972). The second pleopods are each divided into two segments: a basal, slender segment, often with a rudimentary exopod, and a distal segment varying in shape, armature and setation (fig. 2B,C,E,F). Females typically lack first pleopods. However, in some normal (non-parasitized) females, paired first pleopods are often represented by small buds. Paired second pleopods, the right being vestigial, have been observed in females of all but one species (*Sympagurus rutricheles* A. Milne Edwards).

In many species, numerous low, blister-like tubercles may be present on the shield, posterior carapace, second to fifth pereopods, abdominal somites,

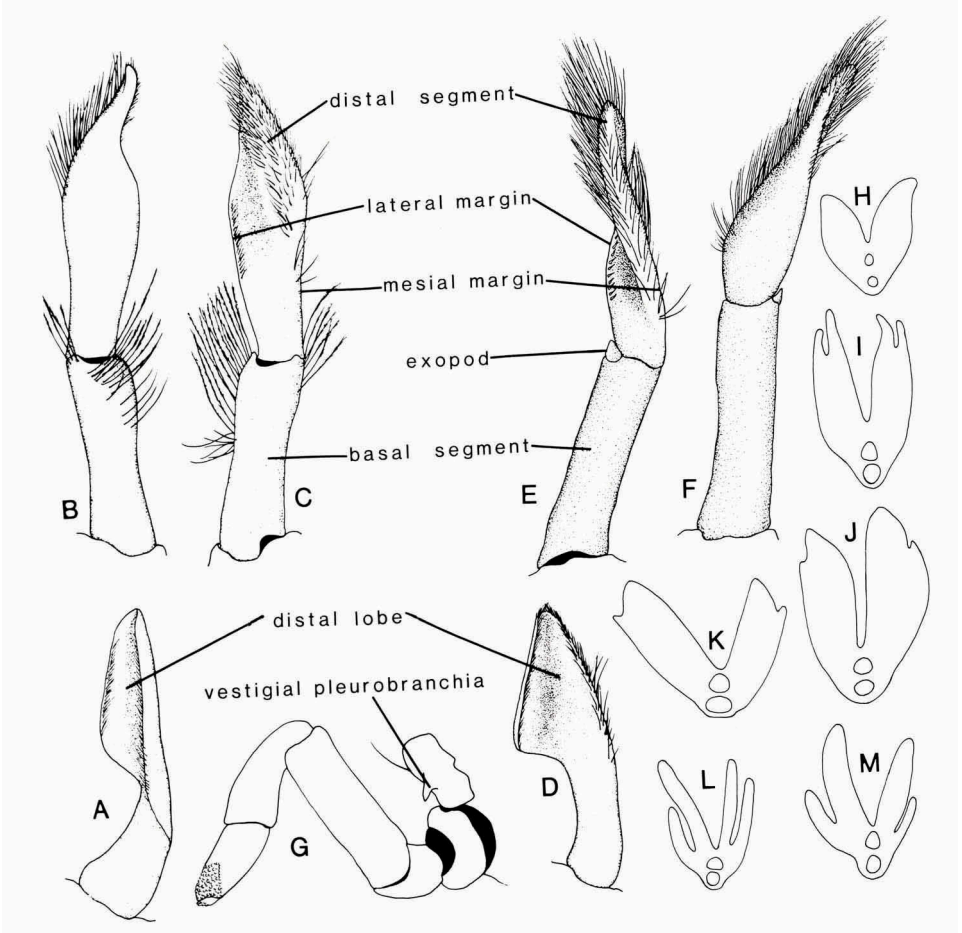

Fig. 2, diagrammatic male left first and second pleopods, left fifth pereopod, and branchiae (transverse section), depicting terminology used in text. A-C, *Parapagurus* Smith: A, first pleopod (mesial view); B, second pleopod (posterior view); C, same (anterior view). D-F, *Strobopagurus* gen. nov.: D, first pleopod (mesial view); E, second pleopod (posterior view); F, same (anterior view). G, fifth pereopod and side of last thoracic somite. H-M, types of branchiae: H, phyllobranchia; I-K, intermediate branchiae; L, M, trichobranchiae.

uropods, telson, and male second pleopods. The shape of the tubercles varies from subcircular to ovate, and often one or more are partially fused.

SYSTEMATIC ACCOUNT

Key to the genera of the family Parapaguridae

1. Corneae present 2

– Corneae absent ..... *Typhlopagurus* De Saint Laurent
2. Rostrum short, not exceeding eye-stalks 3
– Rostrum long, exceeding eye-stalks ..... *Probeebei* Boone
3. Ocular acicles present 4
– Ocular acicles absent ..... *Tylaspis* Henderson
4. Trichobranchiae; lacking vestigial pleurobranchiae; corneae not strongly dilated; antennal peduncles and acicles distinctly overreaching eye-stalks; palm of right cheliped rounded mesially and laterally; males with well developed first and second pleopods (fig. 2B,C) ... *Parapagurus* Smith
– One or more characters not as above 5
5. Shield distinctly broader than long; corneae strongly dilated; lacking epistomial spine; dactyls of ambulatory legs straight or nearly so; males with first pleopod lacking short exopod; second pleopod with short exopod and strongly twisted distal segment (fig. 2E,F) .... *Strobopagurus* gen. nov.
– One or more characters not as above ..... *Sympagurus* Smith

Parapagurus Smith, 1879

Parapagurus Smith, 1879: 50. Type species by monotypy: *Parapagurus pilosimanus* Smith, 1879: 51. Gender: masculine. — De Saint Laurent, 1972:101 (in part).

Diagnosis. — Shield usually well calcified; lateral projections unarmed; ventrolateral margins of shield unarmed. Corneae not strongly dilated. Antennal peduncles and acicles distinctly overreaching eye-stalks. Fourth segment of antennal peduncle unarmed. Epistomial spine, when present, short and straight. Eleven pairs of trichobranchiae (lacking vestigial branchiae on last thoracic somite). Right cheliped elongate; palm rounded mesially and laterally. Left cheliped well calcified. Ambulatory legs long, dactyls curved. Second abdominal somite with left pleuron terminating ventrally in small subtriangular lobe. Males with well developed paired first and second pleopods (fig. 2A-C); first pleopods with elongate subconical or subtubular distal lobe; second pleopods with distal segment twisted.

The following species are assigned to *Parapagurus* Smith: *Parapagurus pilosimanus* Smith, *P. abyssorum* (Filhol), *P. alaminos* Lemaitre, *P. andersoni* Henderson, *P. andreui* Macpherson, *P. benedicti* De Saint Laurent, *P. bouvieri* Stebbing, *P. holthuisi* nom. nov., *P. latimanus* Henderson, *P. microps* De Saint Laurent, and *P. nudus* (A. Milne Edwards).

Distribution. — World-wide.

Remarks. — Although Smith (1879) defined *Parapagurus* particularly on the trichobranchiae of *P. pilosimanus*, he did include a number of additional

possible characters. These were: reduced eyes, length of antennules and antennae, narrowness of sternum between the second and third pereopods, and males with well developed paired first and second pleopods. As more specimens of *P. pilosimanus* were collected, and new species of *Parapagurus* were described, the definition of the genus was expanded (Smith, 1883; Henderson, 1888; Milne Edwards & Bouvier, 1893, 1894a; Alcock, 1905). Among the characters added by these authors were: lack of paired pleopods in females, unpaired left gonopore in females, and the lack of a flagellum on the exopod of the first maxilliped. Following Balss' (1912) unification of *Parapagurus* and *Sympagurus, Parapagurus* was expanded even more to accomodate those species with phyllobranchiae (e.g., Barnard, 1950; Forest, 1955; De Saint Laurent, 1972; McLaughlin, 1974). De Saint Laurent (1972) tentatively divided the species of *Parapagurus* into three informal groups: *pilosimanus, dimorphus*, and *gracilipes*. However, the division was based on characters of the right cheliped, and her groups are of unclear phylogenetic significance.

A re-examination of the characters previously used in the diagnosis of the genus has shown that most are not of diagnostic significance at the generic level. Rather, the concurrent presence of several characters must be used to define the genus. The species of *Parapagurus* exhibit the following characters: 1. trichobranchiate gills, 2. corneae not strongly dilated, 3. antennal peduncles and acicles distinctly overreaching the eye-stalks, 4. palm of right cheliped rounded laterally and mesially, and 5. well-developed, paired first and second pleopods in males. The species of this genus have the deepest bathymetric distributions within the family.

Key to the western Atlantic species of *Parapagurus* Smith

1. Mesial and lateral faces of meri, carpi, and propodi of ambulatory legs armed with small spines ..... *P. abyssorum* (Filhol)
– Mesial and lateral faces of meri, carpi, and propodi of ambulatory legs unarmed 2
2. Telson with symmetrical lobes; scales of propodal rasp of fourth pereopod conical ..... *P. pilosimanus* Smith
– Telson with asymmetrical lobes; scales of propodal rasp of fourth pereopod ovate 3
3. Carpus of left cheliped armed with small spines or tubercles dorsally (more numerous in males than in females); terminal margin of telson armed with long spines ..... *P. alaminos* Lemaitre
– Carpus of left cheliped unarmed or at most with few small tubercles (males and females); terminal margin of telson armed with short spines ..... *P. nudus* (A. Milne Edwards)

Parapagurus pilosimanus Smith, 1879
(figs. 3, 4, 5A, 6, 39A,B)

Parapagurus pilosimanus Smith, 1879: 51 (type locality: off the coast of Nova Scotia); 1881: 428; 1882: 20, pl. 2, figs. 4-4d; Verrill, 1882a: 137; 1883: 61, pl. 8, fig. 5; Smith, 1883: 33, pl. 5, figs. 2-2a, 4-4b, 5, pl. 6, figs. 1-4a, not figs. 3, 3a (see remarks); 1884: 354 (in part; see remarks); Verrill, 1885: 535, pl.8, fig. 28 (in part; see remarks); Smith, 1886: 607 (in part; see remarks); Pocock, 1889: 430; Bourne, 1890: 316; Milne Edwards & Bouvier, 1892a: 1 (in part; see remarks); 1893: 28; 1894a: 64, pl. 9, figs. 1-17; 1894b: 319; Stebbing, 1893: 167; Bouvier, 1896: 128, fig. 10; Calman, 1896: 2; Henderson, 1896: 530; Milne Edwards & Bouvier, 1899: 54; 1900: 187, pl. 24, figs. 1-3 (in part), not pl. 6, fig. 2 [= *Parapagurus abyssorum* (Filhol, 1885a); see remarks]; Whiteaves, 1901: 259; Hansen, 1908: 29; Fowler, 1912: 581; Selbie, 1921: 8, pl. 7, figs. 1-6; Bouvier, 1922: 20; 1940: 128, fig. 85; Rabaud, 1941: 263; Gordan, 1956: 338 (in part; see remarks); Wolff, 1961b: 16; Lemaitre, 1986: 529, figs. 1C,D, 3A-E, 4C,D, 5E,F, 6I,J, 7C,G, 8H, 9F-H.

Eupagurus Jacobii A. Milne Edwards, 1880: 42; 1882: 42; Smith, 1882: 20; Cuénot, 1892: 56.

Pagurus pilimanus : Milne Edwards, 1884a: 176; 1884b: 27; Perrier, 1886: 301, fig. 219; Bouvier, 1888: 246; Cuénot, 1892: 56. [not *Sympagurus pilimanus* (A. Milne Edwards, 1880); see remarks].

Eupagurus jacobii : Henderson, 1888: 86; 1896: 530.

Parapagurus abyssorum Henderson, 1888: 87 (in part), ?not pl. 9, fig. 2. [not *Parapagurus abyssorum* (Filhol,1885a); see remarks].

Parapagurus abyssorum : Milne Edwards & Bouvier, 1893: 31; Bouvier, 1891b: 81; Murray, 1895: 237 (in part); Henderson, 1896: 530 (in part); Bouvier, 1907: 62. [not *Parapagurus abyssorum* (Filhol,1885a)].

?*Parapagurus pilosimanus*: Haddon & Shackleton, 1891: 642; Jourdan, 1891: 270; Alcock, 1905: 99 (in part); Przibram, 1905: 197; Doflein, 1914: 269; Williamson, 1915: 479; Carlgren, 1923: 271; Balss, 1924: 766, fig. 23; 1927: 968, fig. 1070; Boas, 1926: 4; Carlgren, 1928b: 167, fig. 2; Perez, 1934: 20; Forest, 1954: 167; 1955: 100; Springer & Bullis, 1956: 16; Forest, 1958: 99; Füller, 1958: 164, fig. 92; Pike & Williamson, 1958: 2, figs. 1-3; 1960: 539; Forest, 1961: 231; Russell, 1962: 24; Williamson, 1964; De Saint Laurent-Dechancé, 1964: 5, fig. 23; Bullis & Thompson, 1965: 9; Ross, 1967: 306; Williamson & von Levetzow, 1967: 184; Rowe & Menzies, 1968: 549; Zariquiey-Alvarez, 1968: 252; Pilgrim, 1973: 391; Menzies, George, & Rowe, 1973: 100, fig.4-21; Doumenc, 1975: 163; George, 1976: 83; 1979: 61, fig. 3; 1981: 286; Hazlett, 1981: 4; Takeda, 1983: 105, textfig.; Knott & Wendt, 1985: 48. (see remarks).

?*Sympagurus Grimaldii* A. Milne Edwards & Bouvier, 1897: 133; 1898: 1246; 1899: 57, pl. 4, figs. 1-5. (see remarks).

?*Sympagurus grimaldii*: Alcock, 1905: 173; Gordan, 1956: 342.

?*Parapagurus* sp. 1: De Saint Laurent-Dechancé, 1964: 5, figs. 1, 6, 8, 9, 10. (see remarks).

?*Pagurus pilosimanus*: Caullery, 1896: 386; 1922: 9; 1952: 9; Williamson, 1915: 479; 1964: 479. (see remarks).

?Species S. A. 2: Williamson & von Levetzow, 1967: 185, fig. 3h-k. (see remarks).

Parapagurus pilosimanus pilosimanus: De Saint Laurent, 1972: 102, pl. 1, fig. 1 (in part; see remarks); McLaughlin, 1974: 377; Türkay, 1976: 25; Ingle, 1985: 764; De Saint Laurent, 1985: 475.

Parapagurus pilosimanus nudus : De Saint Laurent, 1972: 102, pl. 1, fig. 2 (in part; see remarks).

?not *Parapagurus pilosimanus*: Alcock, 1901: 204; Porter, 1906: 29; Balss, 1912: 96, pl. 11, figs. 1-6; 1913: 50; Terao, 1913: 385; Laurie, 1926: 160; Moore, 1932: 298; Yokoya, 1933: 79; Makarov, 1938: 223, fig. 74; Thompson, 1943: 412; Vinogradov, 1950: 230; Haig, 1955: 17; Moore & Kruse, 1956: 15; Makarov, 1962: 142, fig. 74; Austin, 1985: 642. (see remarks).

not *Parapagurus pilosimanus*: Barnard, 1950: 450, fig. 83a,b (= *Parapagurus bouvieri* Stebbing, 1910); Kensley, 1974: 65 (= *Parapagurus bouvieri* Stebbing, 1910).

not *Parapagurus pilossimanus*: Verrill, 1928: 16 (misspelling of *P. pilosimanus*) (= *Sympagurus pictus* Smith, 1883).

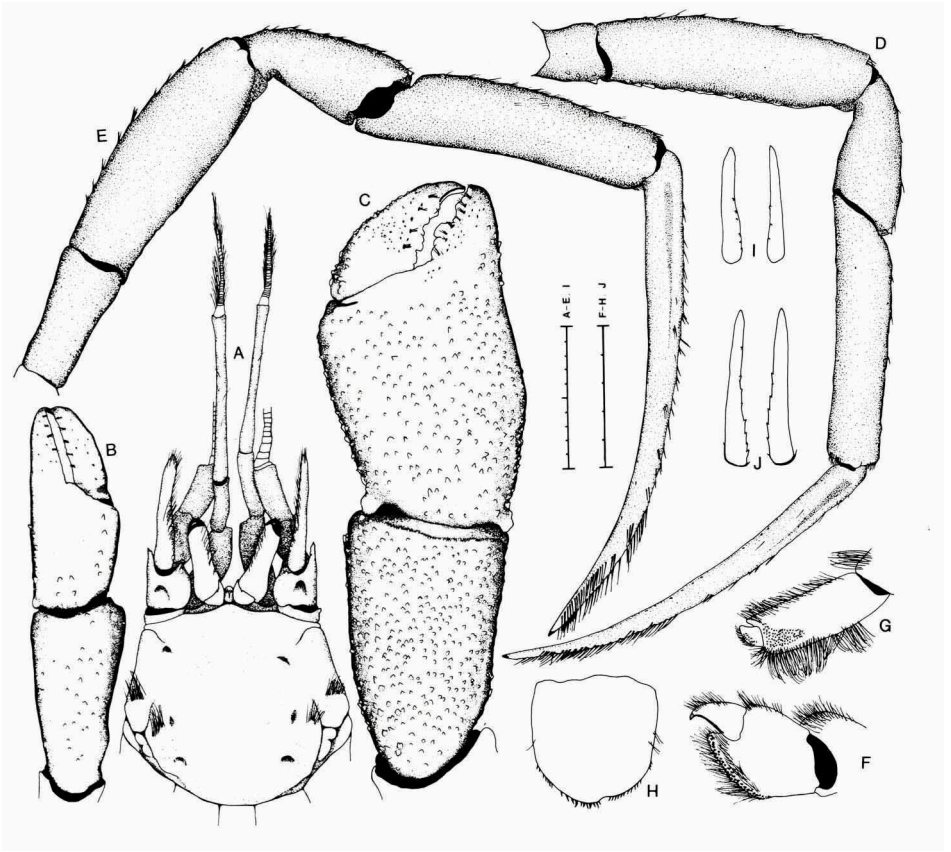

Fig. 3, *Parapagurus pilosimanus* Smith. A, shield and cephalic appendages; B, left chela and carpus; C, right chela and carpus; D, left second pereopod (mesial view); E, left third pereopod (mesial view); F, propodus and dactyl of left fourth pereopod (lateral view); G, propodus and dactyl of left fifth pereopod (lateral view); H, telson (dorsal view); I, denuded antennal acicles (dorsal view); J, denuded antennal acicles (dorsal view). Scales equal 10 mm (A-E, I), and 5 mm (F-H, J). A-I: holotype, USNM 21413. J: ♀ (SL = 9.5 mm), northwestern Atlantic, Advance II station 78-1-9, USNM.

Type material. — Holotype: ♂ (SL=13.1 mm), Guy Cunningham, 42° 41'N, 63° 06'W, 450 m, USNM 21413; Syntype of *Eupagurus jacobii* A. Milne Edwards, 1880: ♀ (SL=3.6 mm), MCZ 2577.

Material examined. — In addition to the material reported by Lemaitre (1986: 529), the following has been examined from the eastern Atlantic: 2 ♂♂, 5 ♀♀, Madeira (RMNH); 11 ♂♂, 10 ♀♀, Selvagens Islands (RMNH); 1 ♂, Canary Islands (RMNH).

Description. — Shield usually as broad as long. Rostrum rounded, slightly overreaching lateral projections, with mid-dorsal 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. Anterolateral margin of branchiostegite unarmed.

Ocular peduncles less than half length of shield, with longitudinal row of setae dorsally; ventrobasal portion of peduncle inflated. Ocular acicles subtriangular, usually terminating in strong simple spine, occasionally bifid; mesial margins convex, lateral margins sloping; separated basally by approximately basal width of one acicle.

Antennular peduncles slender, long, exceeding distal margin of corneae by slightly less than entire length of penultimate segment, with scattered setae. Ultimate segment about 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 one spine proximally.

Antennal peduncles exceeding distal margin of corneae by entire length, or more, of ultimate segment. Flagellum distinctly overreaching right cheliped, with scattered setae less than one flagellar article in length proximally, naked distally. Third to fifth segments with scattered setae. Third segment with strong, ventromesial, distal spine. Second segment with dorsolateral distal angle produced, terminating in strong simple to multifid spine; mesial margin convex, with small tubercle or spine at dorsodistal angle. First segment with small tubercle on lateral face distally; ventromesial angle produced, with one or more small spines. Antennal acicles nearly straight in dorsal view, distinctly overreaching distal margin of corneae; mesial margin setose, unarmed or with one to six small tubercles or spines on proximal half.

Mouth parts as figured (fig. 4A-G). Sternite of third maxilliped with spine on each side of midline. Epistomial spine usually absent.

Chelipeds markedly dissimilar, each usually with carpus and chela covered with dense simple and plumose setae. Right cheliped elongate, proportions influenced by size and sexual dimorphism. Fingers each terminating in calcareous claw, with numerous tufts of setae on dorsal and ventral surfaces; cutting edges each with irregularly sized calcareous teeth; cutting edge of dactyl also with distal row of small corneous spines. Dactyl set at oblique angle to palm; with irregular rows of small tubercles and spines mesially. Palm with dorsal surface with numerous small tubercles or spines; ventral surface usually unarmed. Carpus with numerous small tubercles or spines on all surfaces (less numerous mesially and ventrally). Merus with scattered small tubercles dorsally and laterally; mesial face smooth; ventromesial margin with row of tubercles. Ischium with scattered small tubercles on lateral face; ventromesial margin with row of tubercles; dorsal margin usually with bilobed protuberance. Coxa commonly with small tubercles on ventroproximal angle, and

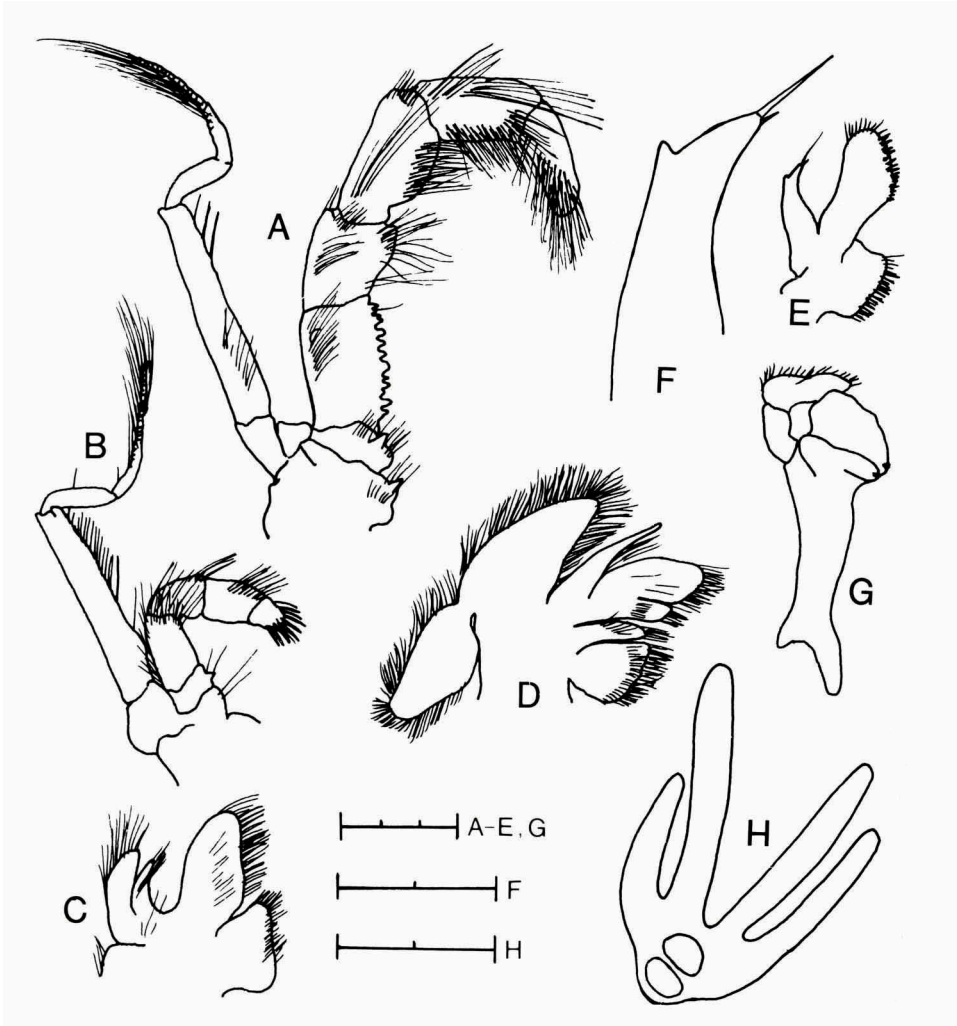

Fig. 4, *Parapagurus pilosimanus* Smith. ♂ (SL = 12.8 mm), norhtwestern Atlantic, Gilliss station 75-8-36, USNM: A-G, mouth parts (left, internal view): A, third maxilliped; B, second maxilliped, C, first maxilliped; D, maxilla; E, maxillule; F, endopod of same; G, mandible; H, branchia (transverse section). Scales equal 3 mm (A-E, G), 1 mm (F), and 2 mm(H).

with ventromesial row of setae.

Left cheliped slender. Fingers each terminating in small corneous claw; dorsal and ventral surfaces with tufts of setae; cutting edges each with row of small corneous teeth. Palm usually smooth, sometimes with row of small tubercles on dorsolateral, dorsomedian, and dorsomesial faces. Carpus and merus subtriangular. Carpus usually with scattered small tubercles or spines dorsally. Merus unarmed dorsally, or with few tubercles; ventromesial margin

with row of tubercles; ventral surface with small tubercles. Ischium with ventromesial row of small tubercles. Coxa with ventromesial row of long setae.

Ambulatory legs similar from right to left; slender, long, exceeding right cheliped; ischium, merus, carpus, and propodus, each with unarmed mesial and lateral faces, and short setae on dorsal margins. Dactyls subequal to combined length of carpi and propodi, most strongly curved in distal half; with dorsodistal and dorsomesial distal row of long setae, and ventromesial row of corneous spinules. Carpus with small dorsodistal spine. Meri of second pereopods each with ventral row of small tubercles; meri of third pereopods unarmed. Anterior lobe of sternite of third pereopods subsemicircular, setose, armed with small subterminal 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 two to three irregular rows of conical scales (individuals SL < 4.0 mm often with ovate scales). Propodal rasp of fifth pereopod forming subtriangular area less than half the length of propodus.

Exopod of left uropod elongate, anterior margin broadly rounded. Telson with terminal margin usually evenly convex, entirely armed with small corneous spines; commonly with very small V-shaped sinus separating generally symmetrical lobes.

Males with paired first and second pleopods well developed. Females usually lacking first pleopods, occasionally with paired or unpaired (left or right) rudimentary first pleopods.

Size. — ♂♂, SL=2.8-16.5 mm; ♀♀, SL=2.7-13.8 mm; ♀♀ (ovigerous), SL=4.9-14.0 mm.

Symbiotic associations. — Usually found living in shelters formed by a species of *Epizoanthus*. Large individuals of *P. pilosimanus* commonly inhabit large colonies of this zoanthid (fig. 5A).

Distribution. — North Atlantic: from southwest of Iceland and the Faeroe Islands (Hansen, 1908) to west of Ireland. Western Atlantic: from off Nova Scotia to Guyana. Eastern Atlantic: from the Bay of Biscay to the Gulf of Guinea. South Atlantic: Tristan da Cunha (Henderson, 1888). Depth range: from 102 m to 3864 m; most frequently found in depths of 400 m to 1400 m.

Affinities. — Among the species of *Parapagurus* Smith from the western Atlantic, this species is most closely allied to *P. nudus* and *P. alaminos*. *P. pilosimanus* can be distinguished from these two species primarily by the shape and armature of the telson, the shape of the scales of the propodal rasp of the fourth pereopod, and the armature of the antennal acicles. The frequency of occurrence of the epistomial spine can also be used as an additional character to separate *P. pilosimanus* from *P. nudus* and *P. alaminos*. The spine is usually absent in *P. pilosimanus*, whereas the spine in the the other two species is

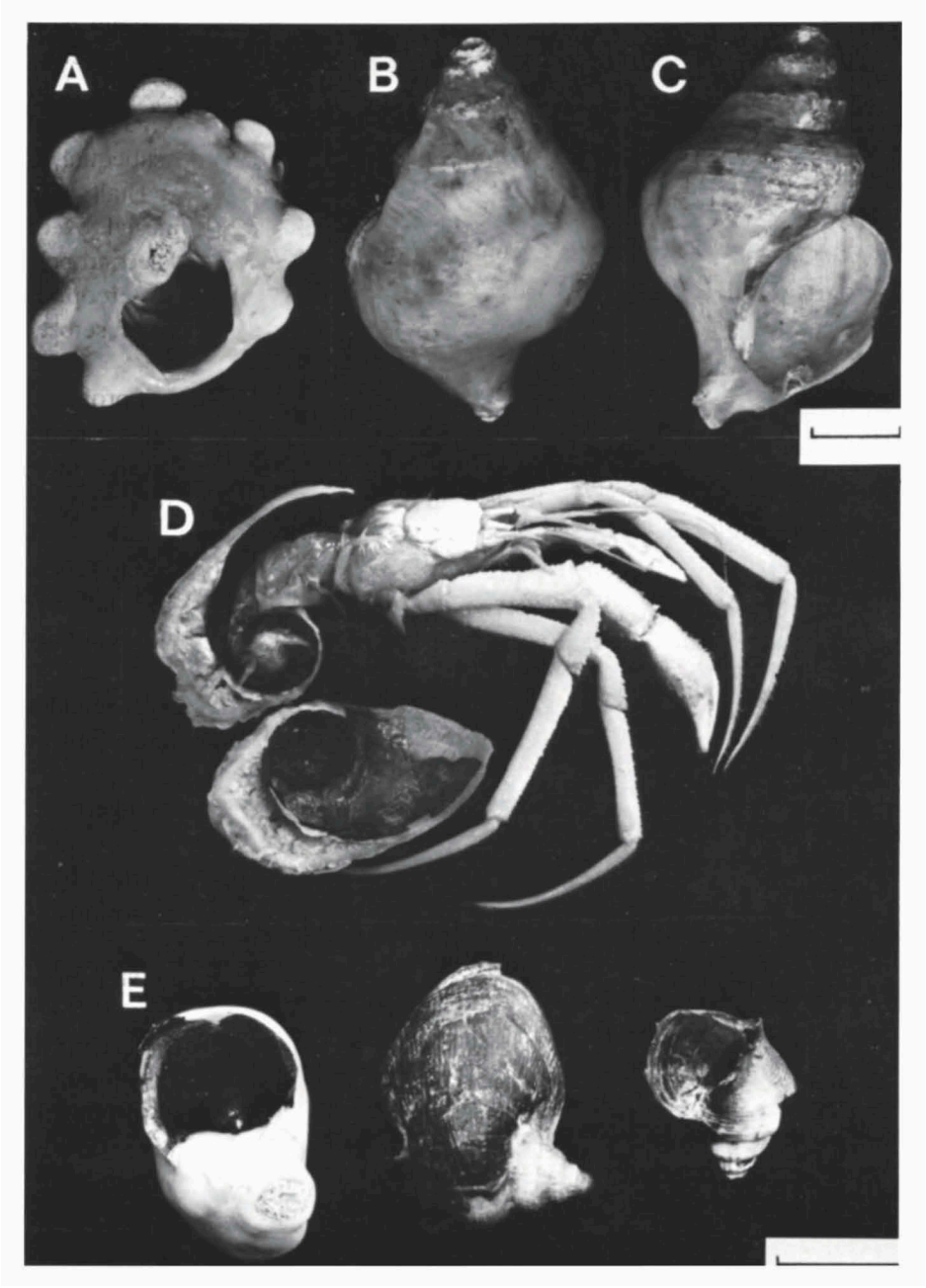

Fig. 5, examples of anthozoan symbionts of species of *Parapagurus* Smith. A, *Epizoanthus* spec. (*P. pilosimanus* Smith); B, actinian on gastropod shell [*P. nudus* (A. Milne Edwards)]; C, same; D, actinian, cut in half [*P. abyssorum* (Filhol)], shown); E, actinian (left), pseudo-shell (center and right) [*P. abyssorum* (Filhol)]. Scales equal 10 mm (A-C), and 20 mm (D, E).

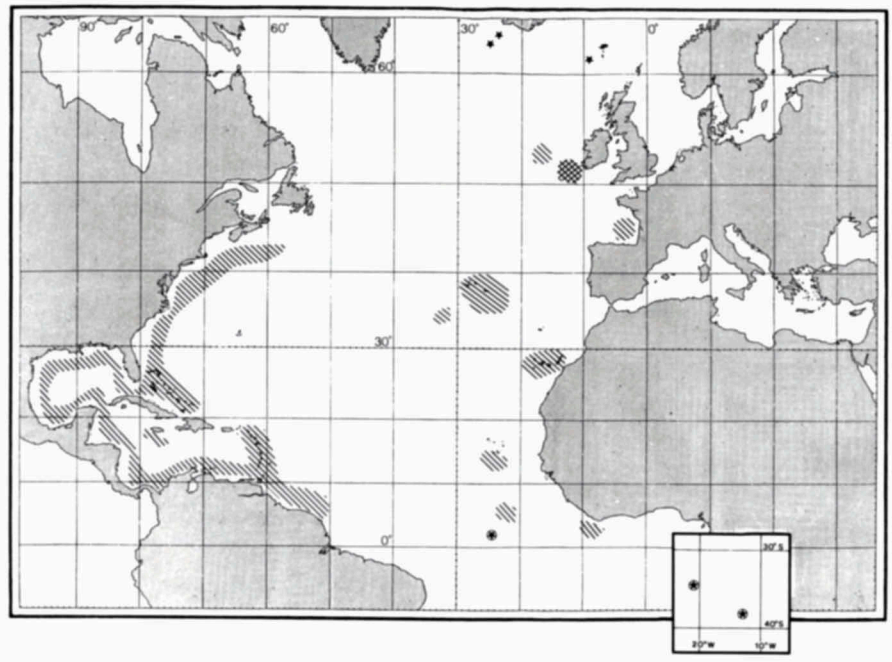

Fig. 6, map showing distribution of *Parapagurus pilosimanus* Smith [hatched area: based on material examined; cross-hatched area: based on Selbie (1921); stars: based on Hansen (1908); circled stars: based on Henderson (1888)].

usually present [see variations in Lemaitre (1986)].

Remarks. — Smith (1879) described this species from one male specimen, but subsequently reported numerous specimens from the northeastern coast of the United States (Smith, 1881, 1882, 1883, 1884, 1886). An examination of most of Smith's material as well as numerous additional specimens collected since then, has made it possible to clearly diagnose his taxon. [In Smith's (1883) plate 6, the legends for figures 2-2a, and figures 3, 3a, were inverted]. It is clear that Smith and other carcinologists confounded several species under the name *Parapagurus pilosimanus*. My examination of Smith's material has revealed that it represents his *P. pilosimanus* for the most part, except for some of the material reported in 1884 and 1886, which also includes specimens of *P. nudus*, and *P. abyssorum* (Filhol). The anthozoans found living symbiotically with Smith's (1884) specimens were reported by Verrill (1885) in association with *P. pilosimanus*. Verrill also confounded Smith's taxon with *P. nudus* and *P. abyssorum*.

In a narrative of the Talisman expeditions to the eastern Atlantic, Milne Edwards (1884a, 1884b) cited *Pagurus pilimanus*, and subsequently Milne Edwards & Bouvier (1900) included the name in the synonymy of *Parapagurus*

pilosimanus. Clearly, Milne Edwards' citation referred to *Parapagurus pilosimanus*, and not to *Sympagurus pilimanus* (A. Milne Edwards).

Henderson (1888) described *P. abyssorum* from specimens collected in both the Atlantic and Indo-West-Pacific regions. He also described a variety, *P. abyssorum* var. *scabra*, for a female specimen from the Atlantic that differed from his typical *P. abyssorum*. Because Milne Edwards & Bouvier (1892a) believed that Smith's *P. pilosimanus* was a highly variable cosmopolitan species they considered Henderson's taxa to be only variants of Smith's taxon. However, in order to include those representatives of Henderson's taxa that occurred at great depths (3650-4060 m) and which differed significantly from his taxon, they retained Henderson's (1888) *abyssorum* as a variety. In her subdivision of *P. pilosimanus*, De Saint Laurent (1972), not realizing that *P. abyssorum* (Filhol) was an available name, reinstated Henderson's variety *scaber*, and ranked both *scaber* and *abyssorum* sensu Henderson as subspecies of *P. pilosimanus*. As previously noted, Henderson's *P. scaber* is a junior synonym of *P. abyssorum* (Filhol). Henderson's *P. abyssorum* is a junior homonym of Filhol's taxon, and as such is a preoccupied name; therefore, Henderson's taxon requires a new name. Henderson's Atlantic material is referrable to *P. pilosimanus* Smith; however, his illustration (pl.9, fig. 6) does not appear to represent this species.

References to *Parapagurus pilosimanus* are found not only in the systematic literature, but also in studies of comparative anatomy (Pilgrim, 1973), anthozoan systematics and symbiotic relationships [Jourdan, 1891; Caullery, 1896, 1922, 1952 (as *Pagurus pilosimanus*); Doflein, 1914; Carlgren, 1923, 1928b; Balss, 1924; Füller, 1958; Ross, 1967; Doumenc, 1975], fecal pellets (Moore, 1932; Moore & Kruse, 1956), and ecology (Menzies et al., 1973). Since it is impossible to determine the identities of the specimens reported by these authors, the specimens are questionably assigned to *P. pilosimanus* Smith.

Among the many samples examined here from throughout the world's oceans, *P. pilosimanus* Smith has not been found outside the Atlantic. Thus the species is herein considered to be restricted to this ocean. Several authors have reported or cited this species from oceans other than the Atlantic (Alcock, 1901; Porter, 1906; Balss, 1912, 1913; Terao, 1913; Laurie, 1926; Verrill, 1928; Yokoya, 1933; Makarov, 1938, 1962; Thompson, 1943; Vinogradov, 1950; Haig, 1955; Gordan, 1956; Russell, 1962; Menzies et al., 1973; Austin, 1985). The descriptions or comments included by these authors are insufficient to establish the identities of their materials, and the specimens have not been available for examination.

A number of authors have suggested that some zoeae collected from the plankton are of *P. pilosimanus* [Williamson, 1915, 1964 (as *Pagurus pil-*

osimanus); Pike & Williamson, 1958, 1960; Williamson & von Levetzow, 1967 (as Species S. A. 2); De Saint Laurent-Dechancé, 1964 (as *Parapagurus* sp. 1)]. However, the complete larval development of any species of *Parapagurus* is unknown. Therefore, assignment of these planktonic zoeae to particular species is speculative.

Sympagurus grimaldii was described by Milne Edwards & Bouvier (1897) from a small male from the Azores. This same specimen was illustrated and used in subsequent reports of this taxon by Milne Edwards & Bouvier (1898, 1899), and listed by Alcock (1905) and Gordan (1956). Milne Edwards & Bouvier's illustrations could represent *P. pilosimanus* Smith, *P. nudus*, or *P. alaminos*. Because Milne Edwards & Bouvier's specimen has not been available for examination, it is questionably considered conspecific with *P. pilosimanus* Smith.

As previously mentioned, De Saint Laurent (1972) tentatively divided *P. pilosimanus* into seven subspecies, three of which occurred in the Atlantic. The examination of the material used by De Saint Laurent has shown that she confounded three species, *P. pilosimanus* Smith, *P. nudus*, and *P. alaminos*, under *P. pilosimanus pilosimanus* and *P. p. nudus*.

Parapagurus alaminos Lemaitre, 1986
(figs. 7, 8, 9)

Parapagurus pilosimanus pilosimanus: De Saint Laurent, 1972: 102, pl. 1, fig. 1 (in part; see *P. pilosimanus* and *P. nudus*).

Parapagurus pilosimanus nudus: De Saint Laurent, 1972: 102, pl. 1, fig. 2 (in part; see *P. pilosimanus* and *P. nudus*).

Parapagurus alaminos Lemaitre, 1986: 527, figs. 1E,F, 2F-J, 4E-H,K, 5C,D, 6D-F, 7A,E, 8D,E, 9D,E (type locality: Alaminos station 71-8-75).

Type material. — Holotype: ♂ (SL=10.3 mm), Alaminos station 71-8-75, 20° 05'N, 92° 20'W, 1307 m, 15 Aug 1971, USNM 228518.

Material examined. — In addition to the material reported by Lemaitre (1986: 527), the following has been examined from the eastern Atlantic: 10 ♂♂, 8 ♀♀, Canary Islands (RMNH).

Diagnosis. — Shield usually as broad as long; rostrum rounded, with mid-dorsal ridge; anterior margins weakly concave; lateral projections broadly rounded. Anterodistal margin of branchiostegite unarmed. Ocular peduncles less than half the length of shield. Antennal peduncles exceeding distal margin of corneae by nearly entire length of ultimate segment. Antennal acicles nearly straight in dorsal view, armed with six to twelve small spines mesially. Mouth parts as figured (fig. 8A-G). Sternite of third maxilliped with spine on each side of midline. Epistomial spine usually present. Dorsal face of carpus of left cheliped armed with irregular rows of small spines or tubercles (less numerous

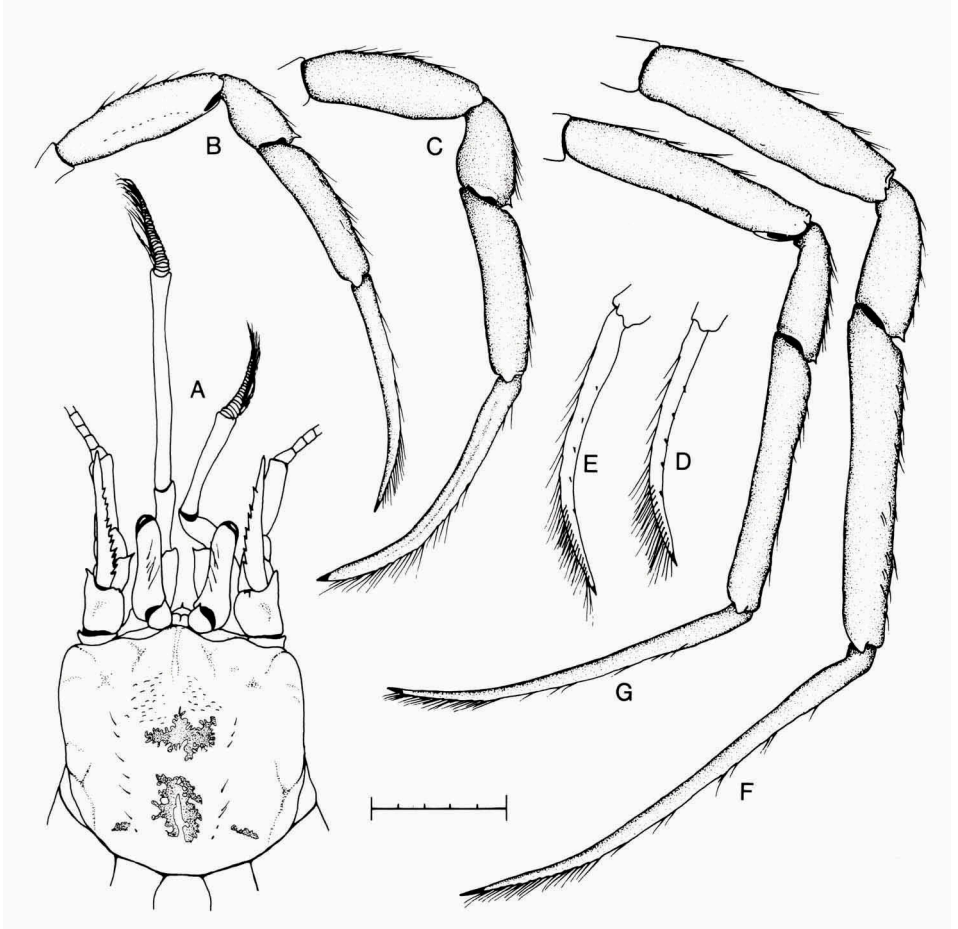

Fig. 7, *Parapagurus alaminos* Lemaitre. A, shield and cephalic appendages; B, right second pereopod (lateral view); C, right third pereopod (lateral view); D, dactyl of right second pereopod (mesial view); E, dactyl of right third pereopod (mesial view); F, right third pereopod (lateral view); G, right second pereopod (lateral view). Scale equals 5 mm. A: ♂ (SL = 9.2 mm), Bahamas, Columbus Iselin station 14, UMML. B-E: ♀ (SL = 5.2 mm), Gulf of Mexico, Alaminos station 71-8-47, TAMU. F, G: ♂(SL = 6.6 mm), Gulf of Mexico, Alaminos station 72-A13-27, TAMU.

in females). Merus, carpus, and propodus of ambulatory legs unarmed except for dorsodistal spine on carpus. Propodal rasp of fourth pereopod with one to three rows of ovate scales. Propodal rasp of fifth pereopod forming subtriangular area about half length of propodus or less. Exopod of left uropod elongate, anterior margin broadly rounded. Telson with shallow, broad sinus separating asymmetrical lobes; terminal margin armed with strong corneous spines.

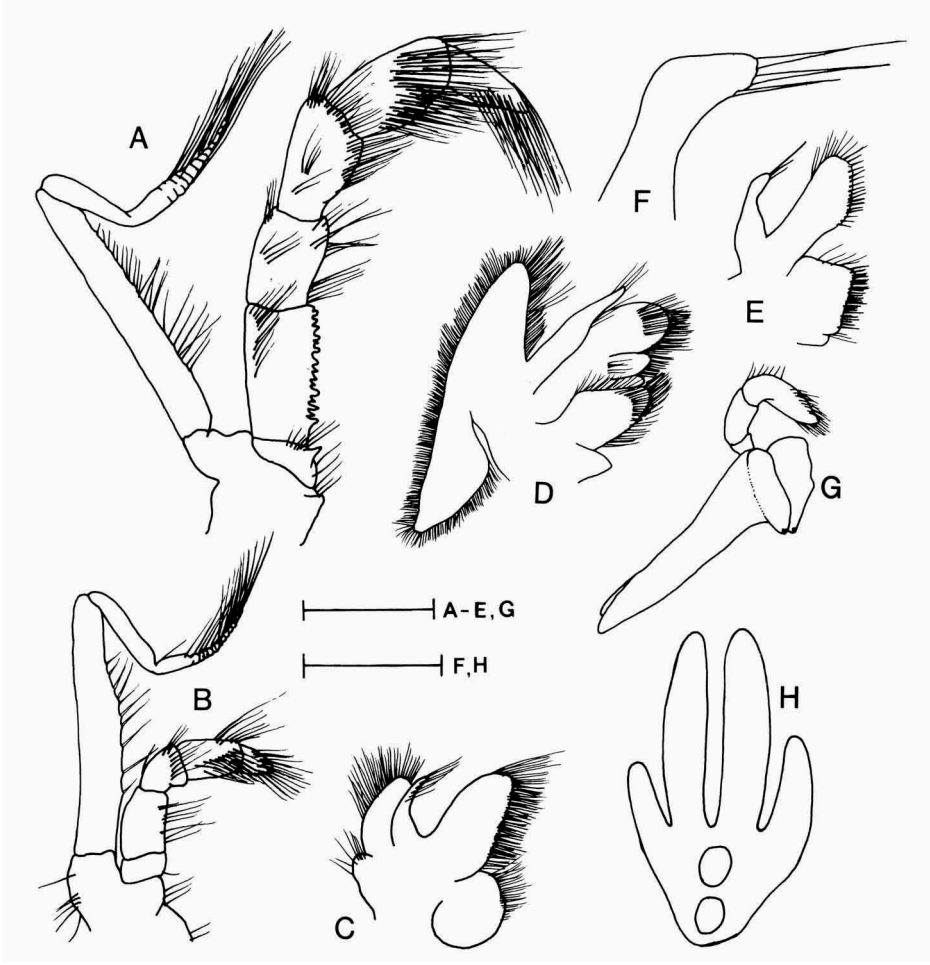

Fig. 8, *Parapagurus alaminos* Lemaitre. ♂ (SL= 7.9 mm), Gulf of Mexico, Oregon station 2574, USNM: A-G, mouth parts (left, internal view): A, third maxilliped; B, second maxilliped; C, first maxilliped; D, maxilla; E, maxillule; F, endopod of same; G, mandible; H, branchia (transverse section). Scales equal 2 mm (A-E, G), and 0.5 mm (F, H).

Size. — ♂♂, SL=2.7-10.0 mm; ♀♀, SL=2.1-8.7 mm; ♀♀ (ovigerous), SL=2.9-9.0 mm.

Symbiotic associations. — Most frequently found living without symbionts. However, one or more anthozoan polyps (actinians or zoanthids) are often found attached to the shells.

Distribution. — Western Atlantic: from off the coast of North Carolina to the southern Caribbean. Eastern Atlantic: from the Azores and Canary Islands to the Gulf of Guinea. Depth range: from 850 m to 3360 m; most frequently found in depths of 1200 m to 1800 m.

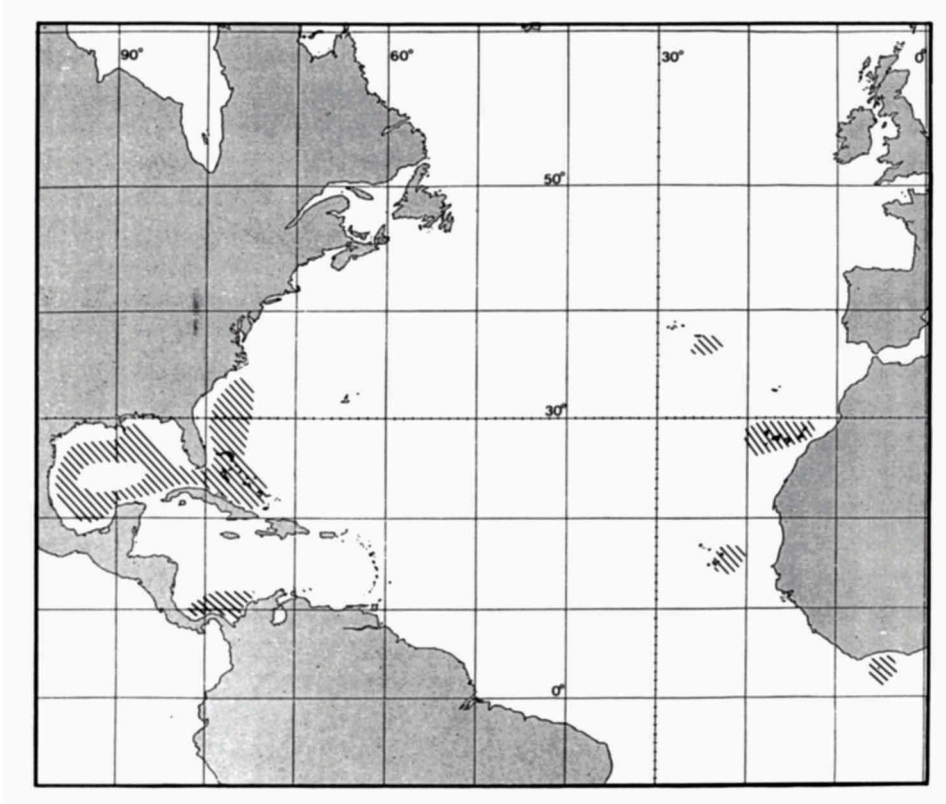

Fig. 9, map showing distribution of *Parapagurus alaminos* Lemaitre (hatched area).

Affinities. — This species is most closely related to *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 of the carpus of the left cheliped. In contrast, the carpus in *P. nudus* is unarmed, or at most bears only a few small tubercles. Females of *P. alaminos* with a weakly armed carpus, are sometimes hard to distinguish from females of *P. nudus*, particularly if only small specimens are available [see variations in Lemaitre (1986)]. In these cases, other characters must be taken into consideration, such as the shape of exopod of the left uropod, armature of telson, and the number of rows of scales on the propodal rasp of the fourth pereopod.

Parapagurus nudus (A. Milne Edwards, 1891)
(figs. 5B, C, 10, 11, 12)

Parapagurus pilosimanus: Smith, 1884: 354 (in part); 1886: 607 (in part).
Sympagurus nudus A. Milne Edwards, 1891: 131 (type locality: SW of Flores, Azores, L'Hiron-

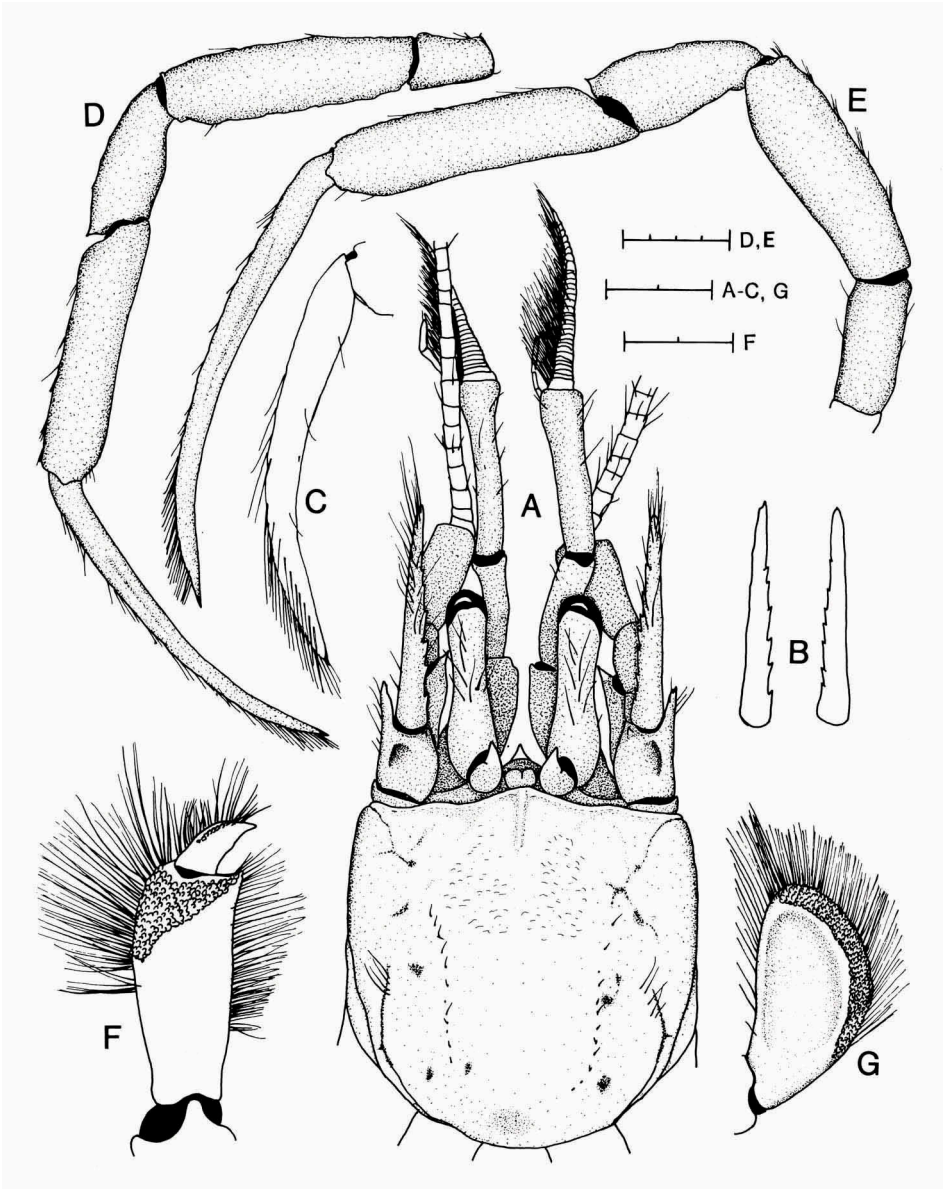

Fig. 10, *Parapagurus nudus* (A Milne Edwards). ♂ (SL = 7.8 mm), northwestern Atlantic, Advance II station 78-1-9, USNM: A, shield and cephalic appendages; B, denuded antennal acicles of same specimen (dorsal view); C, dactyl of right third pereopod (mesial view); D, left second pereopod (lateral view); E, left third pereopod (lateral view); F, propodus and dactyl of left fifth pereopod (lateral view); G, exopod of left uropod (dorsal view). Scales equal 2 mm (A-C, G), 4 mm (D, E), and 1 mm (F).

delle station 213); Bouvier, 1891a: 402; Milne Edwards & Bouvier, 1893: 59; 1894a: 67, pl. 10, figs. 15-26; 1897: 133; 1899: 55; Alcock, 1905: 173; Terao, 1913: 382; Gordan, 1956: 342.

Parapagurus pilosimanus pilosimanus : De Saint Laurent, 1972: 102, pl. 1, fig. 1 (in part; see remarks).

Parapagurus pilosimanus nudus : De Saint Laurent, 1972: 102, pl. 1, fig. 2 (in part; see remarks); Türkay, 1976: 31, fig. 14; De Saint Laurent, 1985: 475.

?*Parapagurus nudus* : Doumenc, 1975: 163. (see remarks).

Parapagurus nudus : Lemaitre, 1986: 533, figs. 1A,B, 2A-E, 4A,B, 5A,B, 6G,H, 7B,F, 8A-C, 9 A,B.

Type material. — Holotype: ♂ (SL=3.3 mm), L'Hirondelle station 213, 39°22.48'N, 33°45.30'W, 1384 m, 2 Aug 1888, MO.

Material examined. — In addition to the material reported by Lemaitre (1986: 533), the following has been examined from the eastern Atlantic: 16 ♂♂, 16 ♀♀, Madeira (RMNH); 18 ♂♂, 11 ♀♀, Selvagens Islands (RMNH); 3 ♀♀, Canary Islands (RMNH).

Description. — Shield usually as broad as long. Rostrum rounded, slightly overreaching lateral projections, with mid-dorsal 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 about half the length of shield or less, with dorsal longitudinal row of setae; peduncles inflated basally. Ocular acicles subtriangular, terminating in strong, occasionally bifid spine; mesial margins convex, lateral margins sloping; separated basally by about basal width of one acicle.

Antennular peduncles slender, long, exceeding distal margin of corneae by entire length or more of ultimate segment. Ultimate and penultimate segments with scattered setae. Ultimate segment nearly twice as long as penultimate. Basal segment with ventromesial, distal spine; mesial face unarmed; lateral face with distal, subrectangular lobe armed with one or more small spines, and one spine proximally.

Antennal peduncles exceeding distal margin of corneae by half or more of length of ultimate segment. Flagellum distinctly overreaching right cheliped, with setae less than one to three flagellar articles in length. Third to fifth segments with scattered setae. Third segment with strong often multifid ventromesial distal spine. Second segment with dorsolateral distal angle produced, terminating in strong multifid spine; mesial margin with small tubercle or spine at dorsodistal angle. First segment occasionally with small tubercle on lateral face distally; ventromesial angle produced, with row of small tubercles. Antennal acicles nearly straight in dorsal view, exceeding distal margin of corneae by one-third or more the length of the acicle; mesial margin setose, usually armed with four to eleven small spines.

Mouth parts as figured (fig.11A-G). Sternite of third maxilliped with spine

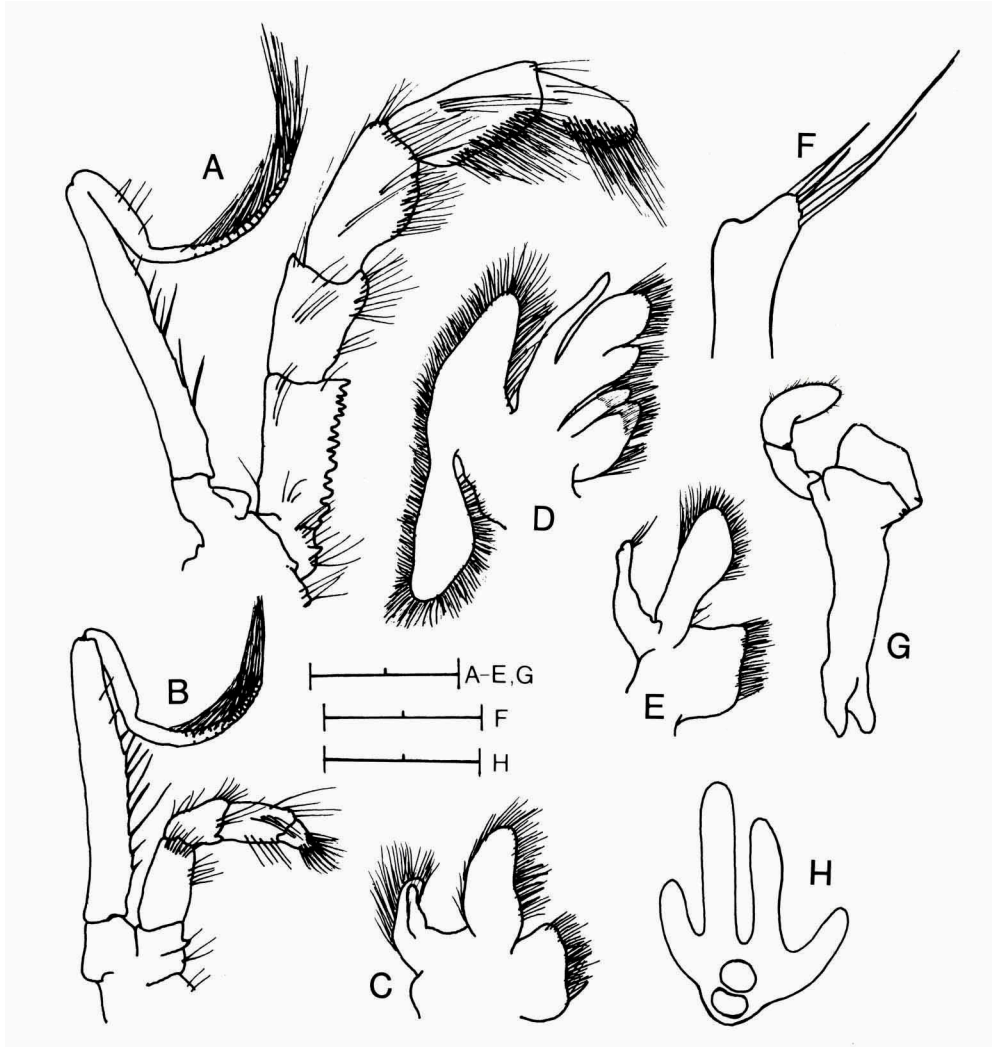

Fig 11, *Parapagurus nudus* (A. Milne Edwards). ♂ (SL = 7.8 mm), northwestern Atlantic, Advance II station 78-1-9, USNM: A-G, mouth parts (left, internal view): A, third maxilliped; B, second maxilliped; C, first maxilliped; D, maxilla; E, maxilule; F, endopod of same; G, mandible; H, branchia (transverse section). Scales equal 2 mm (A-E, G), 0.5 mm (F), and 1 mm (H).

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 proportions by size and sexual dimorphism. Fingers each terminating in small corneous claw; with numerous tufts of setae on dorsal and ventral surfaces; cutting edges each with irregularly sized calcareous teeth;

cutting edge of dactyl also with distal row of small corneous spines. Dactyl set at oblique angle to palm; with dorsomesial and mesial row of small tubercles. Palm with numerous, closely spaced tubercles on dorsal surface, tubercles often less numerous medially; mesial face rounded; ventral surface with scattered, small tubercles. Carpus with numerous small tubercles, less numerous on ventral surface. Merus with numerous tubercles dorsally, and ventromesial row of sharp tubercles or spines. Ischium occasionally with ventromesial row of tubercles; dorsal margin often with bilobed protuberance. Coxa with ventromesial row of setae.

Left cheliped slender. Fingers each terminating in small corneous claw, with dorsal and ventral surfaces with scattered tufts of setae; cutting edges each with row of small corneous spines. Palm usually unarmed except for dorsomesial and dorsolateral row of small tubercles or spines. Carpus and merus subtriangular. Carpus usually unarmed, or at most with few, small tubercles dorsally. Merus and ischium unarmed. Coxa with ventromesial row of setae.

Ambulatory legs similar from right to left, slender, long, distinctly overreaching right cheliped. Ischium, merus, carpus, and propodus each with unarmed mesial and lateral faces, and row of short setae on dorsal margins. Dactyl less than twice as long as propodus, more strongly curved on distal one-third; with dorsodistal and dorsomesial, distal row of long setae, and ventromesial row of corneous spinules. Carpus with simple or bifid, dorsodistal spine. Coxa of second pereopod with ventromesial row of setae. Anterior lobe of sternite of third pereopods subsemicircular, setose, with small, subterminal 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 single row of ovate scales distally, and one to three rows of ovate scales proximally. Propodal rasp of fifth pereopod forming subtriangular area less than half the length of propodus.

Exopod of left uropod usually broad, often subsemicircular; width frequently more than half length. Telson with terminal margin weakly divided into unequal lobes by shallow, broad sinus and with short, corneous spines.

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

Size. — ♂♂, SL=2.2-8.5 mm; ♀♀, SL=2.6-7.1 mm; ♀♀ (ovigerous), SL=3.2-10.4 mm.

Symbiotic associations. — Usually found living without symbionts. However, it is not uncommon to find one or more anthozoan polyps (actinians or zoanthids), attached to the shell (fig. 5B,C).

Distribution. — Western Atlantic: from off Nantucket Island to Guyana. Eastern Atlantic: from the Azores and Canary Islands to the Gulf of Guinea.

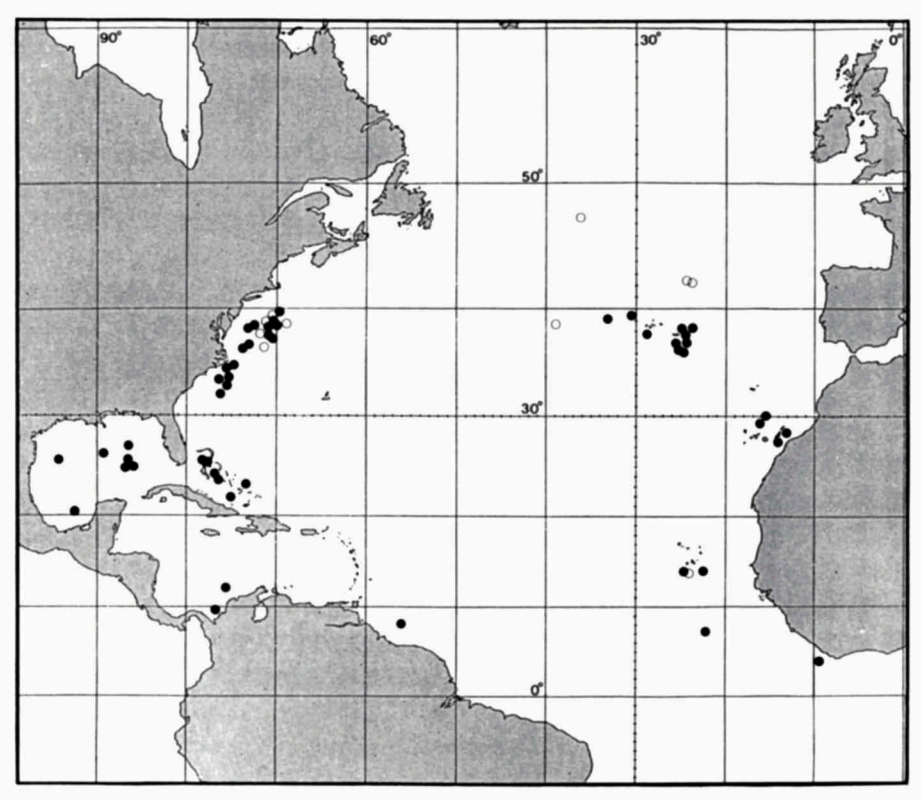

Fig. 12, map showing distribution of *Parapagurus nudus* (A. Milne Edwards), and *Parapagurus abyssorum* (Filhol) (solid circles: *P. nudus*; open circles: *P. abyssorum*).

Depth range: from 630 m to 3864 m; most frequently found in depths of 2400 m to 3600 m.

Affinities. — This species is most closely related to *P. alaminos*. The most reliable character that can be used to separate the two species is the armature of carpus of the left cheliped [see variations in Lemaitre (1986)].

Remarks. — Milne Edwards (1891) described *Sympagurus nudus* from a male specimen from the Azores. He placed this taxon in *Sympagurus* because, in his opinion, the branchiae were not as fully divided as in typical trichobranchiate species. Milne Edwards' specimen is a small individual, and contrary to his interpretation, the branchiae of the specimen are trichobranchiae. Therefore this taxon is retained in *Parapagurus* Smith.

In her division of *P. pilosimanus*, De Saint Laurent (1972) considered Milne Edwards' taxon as a subspecies. However, as mentioned in the remarks under *P. pilosimanus*, she confounded three species (*P. nudus*, *P. alaminos*, and *P. pilosimanus*), under the names *P. p. pilosimanus* and *P. p. nudus*.

In a study of abyssal actinians, Doumenc (1975) mentioned *P. nudus* without providing any information that would enable determination of the identity of his material. His material, therefore, can only be questionably assigned to this species.

Parapagurus abyssorum (Filhol, 1885a)
(figs. 5D, E, 12, 13, 14)

Parapagurus pilosimanus: Smith, 1884: 354 (in part; see *P. pilosimanus*); Smith, 1886: 607 (in part; see *P. pilosimanus*).
Pagurus abyssorum Filhol, 1885a: 132, fig. 1 [type locality: apparently Talisman station 148 (see remarks)]; 1885b: 131, fig. 41. [not *Parapagurus abyssorum* Henderson, 1888 (= *Parapagurus holthuisi* nom. nov.; see remarks)]
Parapagurus abyssorum var.*scabra* Henderson, 1888: 89, pl. 9, fig. 3 (type locality: Challenger station 68); Murray, 1895: 257; Alcock, 1905: 172; Gordan, 1956: 338.
?*Parapagurus abyssorum*: Wood-Mason & Alcock, 1891: 199; Alcock, 1894: 242. (see remarks).
Parapagurus scabra: Milne Edwards & Bouvier, 1892: 13.
Parapagurus pilosimanus Var. *Scabra*: Milne Edwards & Bouvier, 1892a: 2.
Parapagurus pilosimanus var. *abyssorum*: Milne Edwards & Bouvier, 1899: 55, pl. 1, fig. 1; 1900: 191, pl. 24, figs. 4-6; Alcock, 1905: 172; Gordan, 1956: 338.
Parapagurus pilosimanus var. *Abyssorum*: Nobre, 1931: 201, fig. 110; 1936: 126, fig. 103.
Parapagurus pilosimanus scaber: De Saint Laurent, 1972: 102, pl. 1, fig. 3; 1985: 475.
Parapagurus scaber: Lemaitre, 1986: 533, figs. 1G,H, 3F-J, 4I,J, 5G,H, 6A-C,K,L, 7D,H,I, 8F,G, 9C.

Type material. — Holotype of *Pagurus abyssorum* Filhol: ♀ figured by Filhol (1885a: 132, fig. 1), apparently from Talisman station 148, 42°23'N, 21°15'W, 4010 m, 24 Aug 1883; Holotype of *Parapagurus abyssorum* var.*scabra* Henderson: ♀ (SL=11.2 mm), Challenger station 68, 38°03'N, 39°19'W, 3915 m, 24 Jun 1873, BM 1888: 33.
Material examined. — [see Lemaitre (1986: 533, under *Parapagurus scaber* Henderson].

Description. — Shield usually as broad as long. Rostrum rounded or subtriangular, slightly overreaching lateral projections, with mid-dorsal ridge. Anterior margins concave. Lateral projections subtriangular or broadly rounded. Anterolateral margins sloping. Posterior margin broadly rounded. Dorsal surface well calcified, with longitudinal row of short setae on each side of midline. Anterodistal margin of branchiostegite with one or more small spines.

Ocular peduncles less than half the length of shield, with dorsal longitudinal row of setae and often with one to two small spines dorsally; peduncles inflated basally. Ocular acicles subtriangular, usually terminating in simple strong spine; mesial margins convex, lateral margins sloping; separated basally by about basal width of one acicle.

Antennular peduncles slender, long, exceeding distal margin of corneae by nearly entire length of penultimate segment, with scattered setae. Ultimate

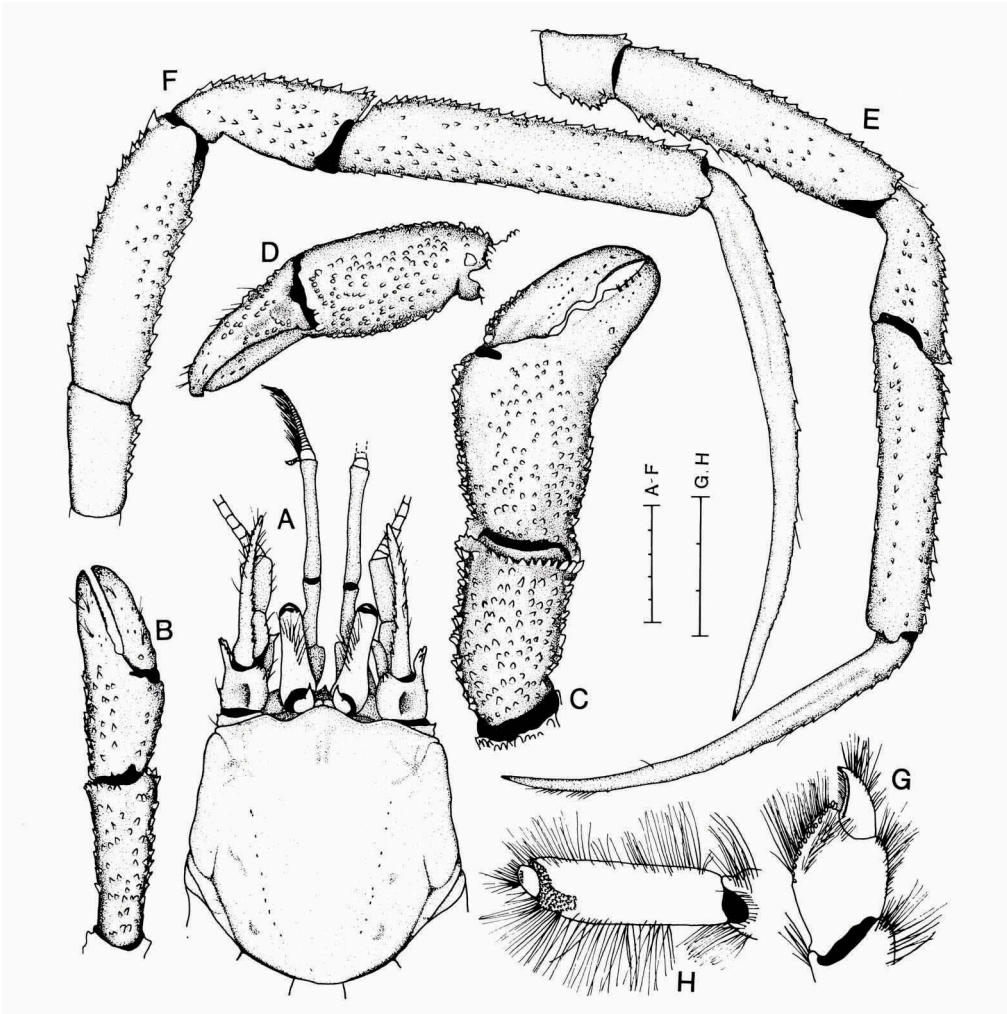

Fig. 13, *Parapagurus abyssorum* (Filhol). ♀ (SL = 11.2 mm), North Atlantic, Challenger station 68, BM 1888:33: A, shield and cephalic appendages; B, left chela and carpus; C, right chela and carpus; D, right chela (mesial view); E, right second pereopod (lateral view); F, right third pereopod (lateral view); G, propodus and dactyl of left fourth pereopod (lateral view); H, propodus and dactyl of left fifth pereopod (lateral view). Scales equal 5 mm (A-F), and 3 mm (G, H).

segment less than twice as long as penultimate, frequently with dorsal row of one to four small spines. Basal segment with ventromesial, distal spine; mesial face unarmed; lateral face with distal, subrectangular lobe armed with one or more small spines, and one spine proximally.

Antennal peduncles exceeding distal margin of corneae by nearly entire length of ultimate segment. Flagellum disctinctly overreaching right cheliped,

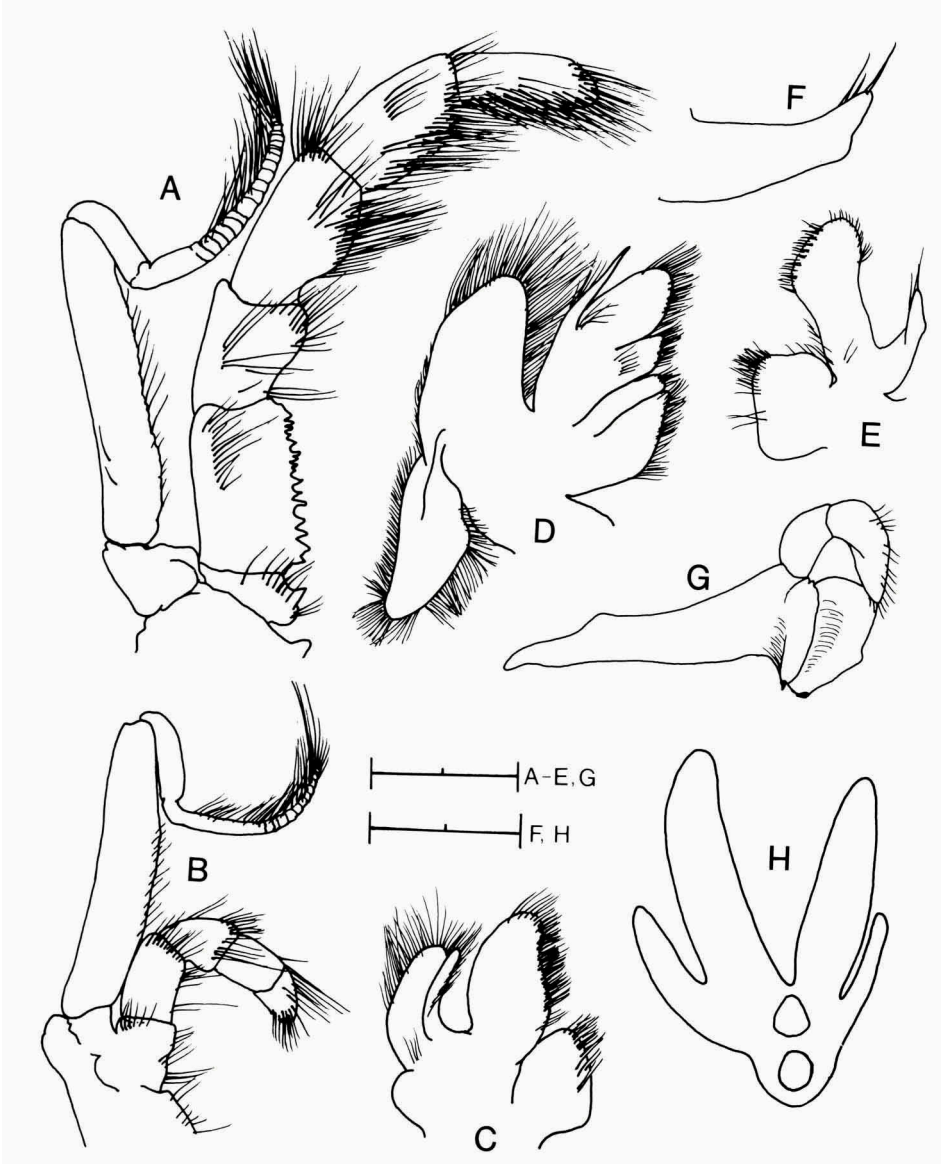

Fig. 14, *Parapagurus abyssorum* (Filhol). ♂ (SL = 8.3 mm), northwestern Atlantic, Albatross station 2037, USNM 168478: A-G, mouth parts (left, internal view): A, third maxilliped; B, second maxilliped; C, first maxilliped; D, maxilla; E, maxilule; F, endopod of same; G, mandible; H, branchia (transverse section). Scales equal 2 mm (A-E, G), and 1 mm (F, H).

with scattered setae about one flagellar article in length or less. Fifth segment with lateral row of long setae. Fourth segment with scattered setae. Third segment with strong, ventromesial, distal, simple or multifid spine. Second

segment with dorsolateral, distal angle produced, terminating in strong, multifid spine; mesial margin convex, with one or more small spines at dorsodistal angle; lateral face with one to two small spines. First segment with small spine on lateral face distally; ventromesial angle produced, with row of one or more small spines. Antennal acicles slender, nearly straight in dorsal view, distinctly overreaching distal margin of corneae; mesial margin setose, armed with five to twenty-five spines.

Mouth parts as figured (fig. 14A-G). Sternite of third maxilliped with spine on each side of midline. Epistomial spine usually absent.

Chelipeds dissimilar, each with carpus and chela covered with moderately dense, simple and plumose setae. Right cheliped elongate, proportions affected by size and sexual dimorphism. Fingers each with tufts of setae on dorsal and ventral surfaces, terminating in acute corneous claw, frequently crossed when closed; cutting edges each with two strong calcareous teeth; cutting edge of dactyl also with distal row of small corneous spines. Dactyl set at oblique angle to palm; with row of tubercles and spines on mesial face proximally. Fixed finger with scattered tubercles on lateral face. Palm with numerous small tubercles or spines on dorsal surface; mesial and lateral face rounded, with irregular rows of small tubercles or spines; ventral surface with scattered tubercles. Carpus with numerous tubercles or spines on dorsal, mesial, and lateral faces; dorsomesial margin often produced distally. Merus with numerous small tubercles dorsally and ventrally; mesial face unarmed except for ventromesial row of tubercles. Ischium usually with two tubercles on dorsal margin; ventromesial margin with row of tubercles. Coxa with several small tubercles or spines ventrally and ventromesial row of setae.

Left cheliped slender. Fingers with scattered tufts of setae on dorsal and ventral surfaces, each terminating in small corneous claw; cutting edges each with small calcareous teeth and row of small corneous teeth. Dactyl with scattered tubercles on dorsolateral face proximally. Palm with irregular rows of small spines on dorsal, mesial and lateral faces. Carpus and merus subtriangular. Carpus with tubercles or spines on lateral and dorsal faces; dorsodistal margin with row of small spines; ventral surface with scattered tubercles. Merus with scattered tubercles and ventromesial row of small spines. Ischium with row of small tubercles or spines on dorsal and mesial faces. Coxa with several small tubercles or spines on ventral face and ventromesial row of setae.

Ambulatory legs similar from right to left, slender, long, overreaching right cheliped by at least half length of dactyls. Dactyl less than twice as long as propodus, more strongly curved on distal one-third; with dorsal row of small spines; with dorsodistal and dorsomesial distal row of moderately long setae, and ventromesial row of well spaced corneous spinules. Merus, carpus, and

propodus each armed on mesial and lateral faces with numerous small tubercles or spines, and with dorsal row of small spines. Propodus also with ventral row of small spines proximally. Carpus with dorsodistal simple to multifid spine. Merus also with ventral row of small spines. Ischium with one or more dorsodistal spines and row of small spines ventrally. Coxa of second and third pereopods each with small spines or tubercles ventromesially. Anterior lobe of sternite of third pereopods subsemicircular, setose, armed with one to five small subterminal spines.

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 one to three irregular rows of lanceolate scales. Propodal rasp of fifth pereopod forming subtriangular area distinctly less than half the length of propodus.

Exopod of left uropod elongate, anterior margin broadly rounded or often subsemicircular. Telson with terminal margin separated into subequal lobes by shallow sinus; armed with short corneous spines.

Male with paired first and second pleopods well developed. Distal segment of second pleopod frequently with longitudinal row of long setae on posterior face. Female usually lacking first pleopods, occasionally with paired or unpaired rudimentary first pleopods.

Size. — ♂♂, SL=7.4-15.0 mm; ♀♀, SL=7.3-13.5 mm; ♀♀ (ovigerous), SL=8.0-13.8 mm.

Symbiotic associations. — Usually found living in shelters formed by colonies of *Epizoanthus* species. The colonies associated with *P. scaber* frequently have coarse surfaces. The coarseness of the surface results from the incorporation by the polyp of sand grains into its walls. *P. abyssorum* is also sometimes associated with actinians (fig. 5D,E).

Distribution. — North Atlantic, including northeastern coast of United States. Eastern Atlantic: from the Azores to Cape Verde Islands. Depth range: from 2500 m to 4360 m; most frequently found in depths of 3800 m to 4200 m.

Affinities. — This species can be immediately distinguished from other Atlantic species of *Parapagurus* by the armature of the ambulatory legs and anterior margin of the branchiostegite. It appears that *P. abyssorum* is most closely related to the eastern Pacific species *P. holthuisi* nom. nov. and *P. microps*, which also have a somewhat similar ornamentation on the ambulatory legs.

Remarks. — Milne Edwards & Bouvier (1900) included in their synonymy of *Parapagurus pilosimanus* var. *abyssorum*, a name mentioned by Filhol (1885b) as *Pagurus abyssorum*. From the description and information given by these authors, it is clear that they were not referring to Henderson's (1888)

eastern Pacific taxon, *Parapagurus abyssorum*, a junior homonym of *P. abyssorum* (Filhol). Because Henderson's taxon is a preoccupied name it has been given a new name, *P. holthuisi* (see remarks under *P. pilosimanus*). As previously indicated, *P. abyssorum* (Filhol) is the senior synonym of *P. scaber* Henderson. Although Filhol (1885b: 131, fig.41) did not include sufficient information on his taxon, it has recently been discovered that in an earlier publication (1885a) this same figure was accompanied by an indication, namely it was proposed "in association with an illustration of the taxon being named" [Art. 12 (b) 7, of the International Code of Zoological Nomenclature]. Thus, Filhol's name is available and is the senior synonym for this taxon. The female used by Filhol (1885a) in his description of *Pagurus abyssorum* appears to be from Talisman station 148, as this station is listed by Sanderson Smith (1889: 985). Considerable confusion about station data of the Talisman exists. For example, in an hectographed list of the stations for the 1883 cruise, Milne Edwards lists only 141 stations; his station 134 is equivalent to Sanderson Smith's station 147. Sanderson Smith's station 148 does not appear in Milne Edwards' list. It is probable that Milne Edwards' station 134 is a combination of Sanderson Smith's stations 147 and 148, which differ in position and depth, but are otherwise very similar (L. B. Holthuis, personal communication). The holotype of *Pagurus abyssorum* Filhol, is the figured specimen from Talisman station 148 (sensu Smith), or station 134 (sensu Milne Edwards). It is probable that one of the two female specimens (USNM 22915) in the National Museum of Natural History is Filhol's type; however, it is impossible to determine which specimen was used by Filhol. Thus, the holotype of *Pagurus abyssorum* Filhol, 1885a, must be considered (by monotypy) the specimen depicted in his figure 1.

Wood-Mason & Alcock (1891), and Alcock (1894), reported *Parapagurus abyssorum* from the Indian Ocean. From the information provided by these authors it is not possible to establish the identity of the material. It is unlikely, however, that it represents *P. abyssorum* (Filhol); therefore, it is questionably assigned to this species.

Strobopagurus gen. nov.

Parapagurus: De Saint Laurent, 1972: 101 (in part).

Diagnosis. — Shield distinctly broader than long, weakly calcified; lateral projections unarmed; ventrolateral margins unarmed. Eye-stalks stout. Corneae strongly dilated. Antennal peduncles and acicles overreaching eyestalks. Fourth segment of antennal peduncle unarmed. Epistomial spine ab-

sent. Eleven pairs of phyllobranchiae or intermediate branchiae. Right cheliped elongate, often slender; palm rounded mesially, with weakly to well delimited dorsolateral margin. Left cheliped usually weakly calcified on merus, carpus, and often proximal portion of palm. Ambulatory legs moderately long, dactyls straight or nearly so. Second abdominal somite with left pleuron terminating ventrally in small subtriangular lobe. Males with well developed paired first and second pleopods (fig. 2D-F); first pleopods with short, broad subtriangular distal lobe; second pleopods with rudimentary exopod and strongly twisted distal segment.

The following species are assigned to *Strobopagurus* gen. nov.: *Parapagurus gracilipes* (A. Milne Edwards), *P. kilburni* Kensley, and *P. sibogae* De Saint Laurent.

Distribution. — Eastern Atlantic and Indo-West Pacific.

Etymology. — *Strobopagurus* is from the Greek *strobos*, meaning anything twisted, and refers to the twisted condition of the second pleopods in males. Gender: masculine.

Remarks. — Species of *Strobopagurus* are set apart from those of *Parapagurus* and *Sympagurus* by the characteristics of the shield, eye-stalks, right cheliped, ambulatory legs, and in males, the first and second pleopods.

Type species. — *Sympagurus gracilipes* A. Milne Edwards, 1891: 132.

Sympagurus Smith, 1883, reinstated

Sympagurus Smith, 1883: 37. Type species by monotypy: *Sympagurus pictus* Smith, 1883: 37. Gender: masculine.
Parapagurus: De Saint Laurent, 1972: 101 (in part).

Diagnosis. — Shield weakly or well calcified; lateral projections unarmed or with small spine or tubercle; ventrolateral margins of shield frequently with small spine. Corneae reduced or dilated. Fourth segment of antennal peduncle unarmed or with dorsolateral distal spine. Epistomial spine, when present, straight or curved upwardly. Eleven or twelve pairs of branchiae (trichobranchiae, phyllobranchiae or intermediate branchiae; twelfth pair vestigial on last thoracic somite). Right cheliped elongate; palm and fixed finger rounded laterally or with well delimited dorsolateral margin. Left cheliped with merus and carpus frequently weakly calcified. Ambulatory legs moderately long, with curved dactyls. Second abdominal somite with left pleuron terminating ventrally in small subtriangular lobe. Males with or without paired first pleopods; second paired pleopods present, variable.

Sympagurus acinops spec. nov.
Sympagurus acutus acutus (De Saint Laurent, 1972) comb. nov.
Sympagurus a. bicarinatus (De Saint Laurent, 1972) comb. nov.
Sympagurus a. hirsutus (De Saint Laurent, 1972) comb. nov.
Sympagurus affinis (Henderson, 1888) comb. nov.
Sympagurus africanus (De Saint Laurent, 1972) comb. nov.
Sympagurus bicristatus (A. Milne Edwards, 1880)
Sympagurus gracilis (Henderson, 1888) comb. nov.
Sympagurus indicus (Alcock, 1905) comb. nov.
Sympagurus boletifer (De Saint Laurent, 1972) comb. nov.
Sympagurus brevipes (De Saint Laurent, 1972) comb. nov.
Sympagurus chuni (Balss, 1911) comb. nov.
Sympagurus curvispina (De Saint Laurent, 1974) comb. nov.
Sympagurus dimorphus (Studer, 1883) comb. nov.
Sympagurus diogenes Whitelegge, 1900
Sympagurus dofleini (Balss, 1912) comb. nov.
Sympagurus haigae (De Saint Laurent, 1972) comb. nov.
Sympagurus hobbiti (Macpherson, 1983b) comb. nov.
Sympagurus macrocerus (Forest, 1955) comb. nov.
Sympagurus minutus (Henderson, 1896) comb. nov.
Sympagurus monstrosus (Alcock, 1894)
Sympagurus orientalis (De Saint Laurent, 1972) comb. nov.
Sympagurus pacificus (Edmondson, 1925)
Sympagurus pictus Smith, 1883
Sympagurus pilimanus (A. Milne Edwards, 1880)
Sympagurus planimanus (De Saint Laurent, 1972) comb. nov.
Sympagurus rugosus (De Saint Laurent, 1972) comb. nov.
Sympagurus rutricheles A. Milne Edwards, 1891
Sympagurus sinensis (De Saint Laurent, 1972) comb. nov.
Sympagurus spinimanus (Balss, 1911) comb. nov.
Sympagurus trispinosus (Balss, 1911) comb. nov.
Sympagurus tuberculosus (De Saint Laurent, 1972) comb. nov.

Table 1. List of species and subspecies assigned to *Sympagurus* Smith, 1883.

The species and subspecies of *Sympagurus* are listed in Table 1.

Distribution. — World-wide.

Remarks. — As defined in this paper, *Sympagurus* contains twenty-nine species and three subspecies. Three of De Saint Laurent's subspecies are elevated to specific rank; these are: *S. bicristatus* (A. Milne Edwards), *S. gracilis* (Henderson), and *S. indicus* (Alcock). Six species occur in the western Atlantic: *S. pictus* Smith, *S. acinops* spec. nov., *S.* bicristatus, *S.* gracilis, *S. dimorphus* (Studer), and *S. pilimanus* (A. Milne Edwards).

Key to the western Atlantic species of *Sympagurus*

1. Corneae reduced ..... *S. acinops* spec. nov.
– Corneae dilated 2

2. Right chela rounded dorsolaterally 3
– Right chela with well-delimited, dorsolateral margin 4
3. Dactyl of fourth pereopod distinctly longer than propodal rasp ..... *S. pictus* Smith
– Dactyl of fourth pereopod distinctly shorter than propodal rasp ..... *S. pilimanus* (A. Milne Edwards)
4. Vestigial pleurobranchiae present; gills trichobranchiate ..... *S. dimorphus* (Studer)
– Vestigial pleurobranchiae absent; gills phyllobranchiate 5
5. Antennal acicles with mesial spines set at 45° angle to longitudinal axis of acicle; ventromesial face of right chela rounded ..... *S. gracilis* (Henderson)
– Antennal acicles with mesial spines set at 90° angle to longitudinal axis of acicle, at least distally; ventromesial face of right chela with well delimited margin ..... *S. bicristatus* (A. Milne Edwards)

Sympagurus pictus Smith, 1883
(figs. 15-17, 18B, 19, 39C, D, 40D)

Eupagurus pilimanus A. Milne Edwards, 1880: 43 (in part). (see remarks)
Parapagurus sp. nov.: Verrill, 1882b: 225.
Sympagurus pictus Smith, 1883: 37 (in part), pl. 5, figs. 3,3a, 5-8, not figs. 2,2a [= *Parapagurus pilosimanus* Smith, 1879] (type locality restricted by lectotype selection: off Martha's Vineyard, U. S. Fish Commission station 924); Verrill, 1883: 50, pl. 8, fig. 4; Smith, 1884: 354, pl. 4, fig. 3; Verrill, 1885: 554; Smith, 1886: 615; Milne Edwards & Bouvier, 1893: 60; 1894a: 67; 1897: 133; 1899: 56; Alcock, 1905: 172; Fowler, 1912: 582; Edmondson, 1925: 29; Gordan, 1956: 342; Bullis & Thompson, 1965: 10.
Eupagurus (*Sympagurus*) *pilimanus*: Milne Edwards & Bouvier, 1893: 63. [not *Sympagurus pilimanus* (A. Milne Edwards, 1880)]
Parapagurus pictus: Balss, 1924: 767; Gordan, 1956: 338; Füller, 1958: 164, fig. 100; De Saint Laurent, 1972: 104.
Parapagurus pilimanus: Takeda, 1983: 104, textfig. [not *Sympagurus pilimanus* (A. Milne Edwards, 1880)]
not *Parapagurus pictus*: Hazlett, 1966: 88 [= *Sympagurus pilimanus* (A. Milne Edwards, 1880)].

Type material. — Lectotype (here selected): ♂ (SL=9.2 mm), U. S. Fish Commission station 924, 39 57.30'N, 70 46'W, 288 m, 16 July 1881, USNM 39980.

Material examined. — Western Atlantic: 5 ♂♂, 5 ♀♀, northwestern Atlantic (USNM); 159 ♂♂, 563 ♀♀, Gulf of Mexico (TAMU, UMML, USNM); 24 ♂♂, 18 ♀♀, Caribbean Sea and southwestern Atlantic (RMNH, UMML, USNM).

Description. — Shield distinctly broader than long; in small specimens (SL<5.0 mm) about as broad as long. Rostrum subtriangular, reaching beyond lateral projections, with mid-dorsal ridge. Anterior margin weakly concave. Lateral projections broadly rounded, frequently terminating in small

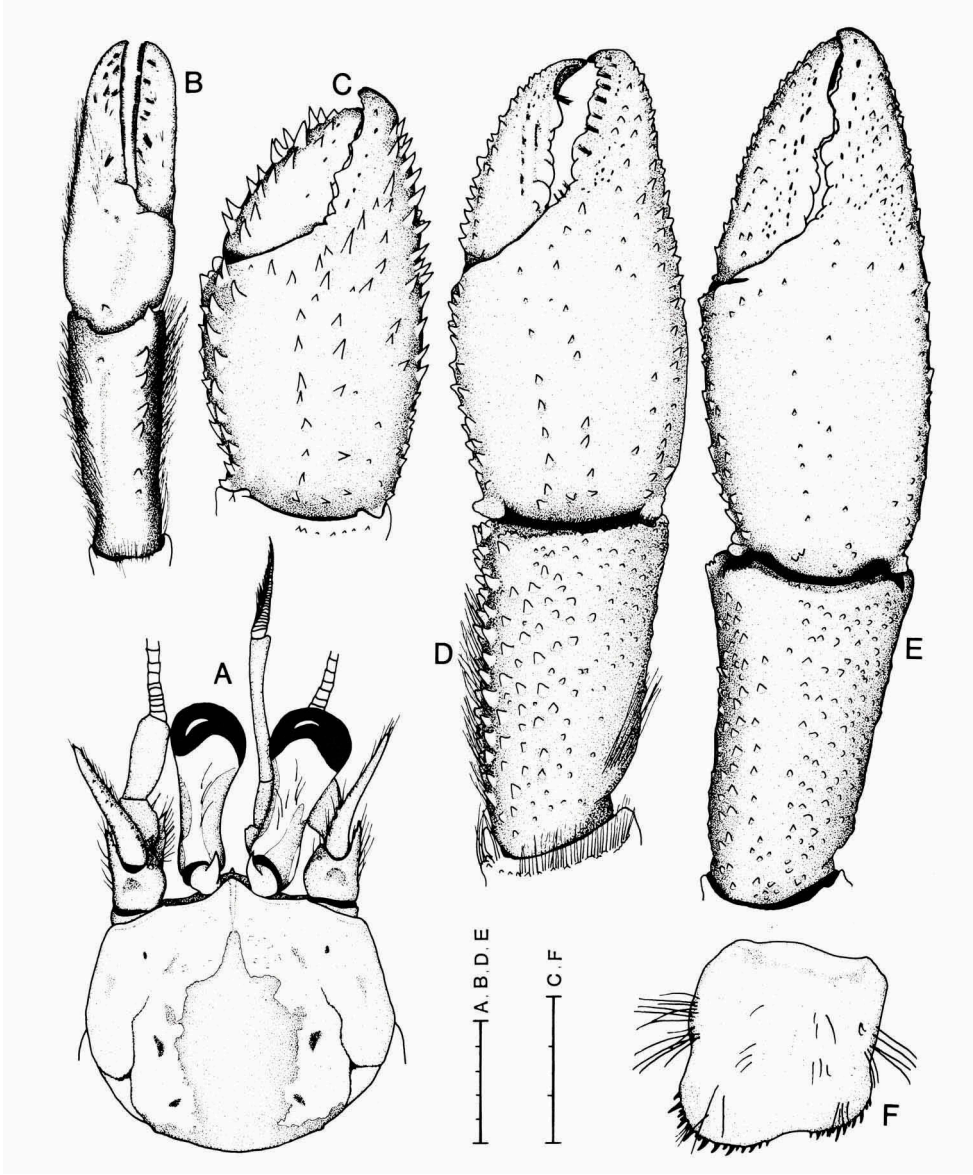

Fig. 15, *Sympagurus pictus* Smith. A, shield and cephalic appendages; B, left chela and carpus; C, right chela of female; D, right chela and carpus of male; E, right chela and carpus of female; F, telson (dorsal view). Scales equal 5 mm (A, B, D, E), and 3 mm (C, F). A, E, F: ♀ (SL = 10.5 mm), Gulf of Mexico, Alaminos station 71-7, TAMU. B, D: lectotype, USNM 39980. C, paralectotype, northwestern Atlantic, U.S. Fish Commission station 924, USNM.

tubercle. Anterolateral margins sloping. Posterior margin broadly rounded. Dorsal surface usually naked and weakly calcified on median region (see

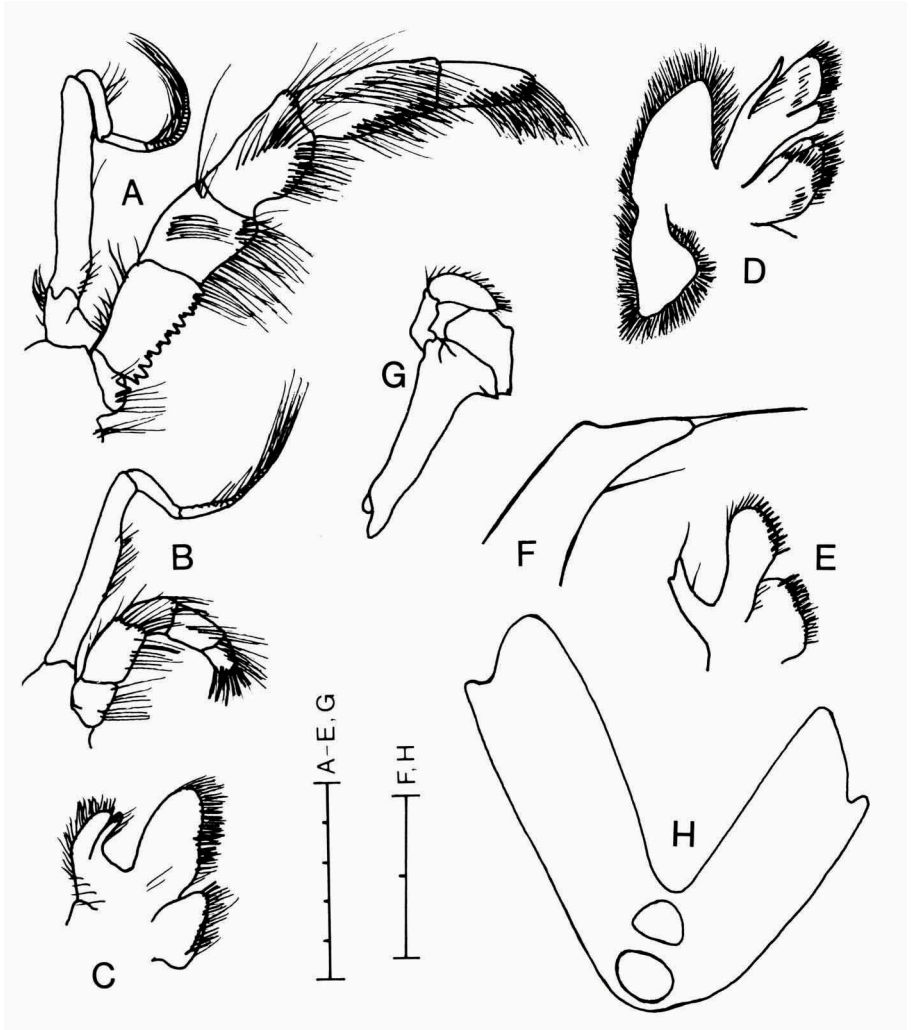

Fig. 16, *Sympagurus pictus* Smith. ♀ (SL = 10.5 mm), Gulf of Mexico, Alaminos station 71-7-56, TAMU: A-G, mouth parts (left, interal view): A, third maxilliped; B, second maxilliped; C, first maxilliped; D, maxilla; E, maxillule; F, endopod of same; G, mandible; H, branchia (transverse section). Scales equal 5 mm (A-E, G), and 1 mm (F, H).

variations). Anterodistal margin of branchiostegite unarmed.

Ocular peduncles more than half the length of shield, weakly calcified on mesial and lateral faces, with dorsal longitudinal row of setae. Corneae strongly dilated. Ocular acicles subtriangular, terminating in strong spine, separated basally by about the basal width of one acicle; mesial margins convex, lateral margins sloping.

Antennular peduncles slender, short, exceeding distal margin of corneae by

less than length of ultimate segment. Ultimate segment naked, less than twice as long as penultimate. Penultimate segment with scattered setae. Basal segment with strong ventromesial spine, simple or bifid; lateral face with unarmed, subrectangular, distal lobe, and one spine proximally.

Antennal peduncles usually not exceeding distal margin of corneae. Flagellum naked, distinctly overreaching right cheliped. Fifth to third segments with scattered setae. Third segment also with strong ventromesial distal spine. Second segment with dorsolateral distal angle produced, terminating in strong, multifid spine; mesial margin convex, with small spine or tubercle at dorsodistal angle. First segment unarmed; ventromesial angle produced, with row of small spines or tubercles. Antennal acicles sinuous in dorsal view, not exceeding distal margin of corneae; mesial margins setose, with small tubercles or spines.

Mouth parts as figured (fig. 16A-G). Sternite of third maxilliped with spine on each side of midline. Epistome usually unarmed or occasionally with one to two straight spines.

Chelipeds markedly dissimilar. Right cheliped elongate, usually densely covered with simple and plumose setae, proportions and armature strongly affected by size and sexual dimorphism (see variations, p. 77). Fingers terminating in corneous claws usually crossing when closed; dorsal and ventral surfaces with scattered tufts of setae; cutting edges each with several unequal calcareous teeth. Dactyl set at oblique angle to palm; cutting edge with distal row of small corneous teeth; mesial face armed with weak to strong spines. Palm with two dorsomedian rows of small spines; mesial and lateral faces rounded, with weak to strong spines; ventral surface usually unarmed. Carpus with numerous tubercles or spines dorsally; mesial face strongly sloping, with ventromesial row of tubercles or spines; lateral face gradually sloping, with scattered small tubercles. Merus with ventromesial row of tubercles or spines. Coxa with ventromesial row of long setae.

Left cheliped slender, usually well calcified, covered with moderately dense, simple and plumose setae. Fingers terminating in corneous claws, dorsal and ventral surfaces with scattered tufts of setae; cutting edges each with row of small calcareous teeth and row of small corneous teeth. Dactyl unarmed. Carpus and merus subtriangular. Carpus with row of weak to strong spines dorsally; with small spine on distal margin laterally. Merus with row of small tubercles dorsally, and row of small spines ventromesially. Ischium with row of small spines ventromesially. Coxa with ventromesial row of long setae.

Ambulatory legs similar from right to left, usually overreaching right cheliped. Dactyl shorter than length of propodus, weakly curved on distal one-third, nearly straight proximally, terminating in corneous claw; with dorsodistal row of long setae, and several short rows of long setae on dorsomesial distal

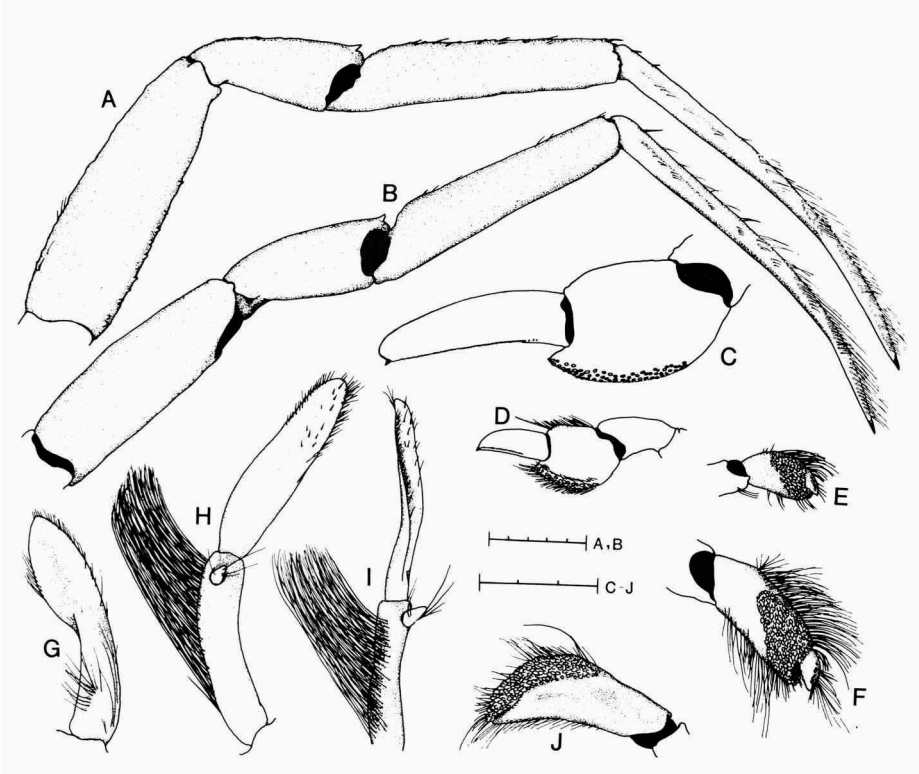

Fig. 17, *Sympagurus pictus* Smith. A, left second pereopod (mesial view); B, left third pereopod (mesial view); C, denuded propodus and dactyl of left fourth pereopod (lateral view, female); D, propodus and dactyl of left fourth pereopod (lateral view, male); E, propodus and dactyl of left fifth pereopod (lateral view, same male); F, propodus and dactyl of left fifth pereopod (lateral view); G, male left first pleopod (mesial view); H, male left second pleopod (anterior view); I, same (lateral view); J, exopod of left uropod (dorsal view). Scales equal 5 mm (A, B), and 3 mm (C-J). A-C: ♀ (SL = 10.5 mm), Gulf of Mexico, Alaminos station 71-7-56, TAMU. D, E, J: paralectotype, USNM 7306. F: lectotype, USNM 39980. G-I: ♂ (SL= 15.0 mm), Gulf of Mexico, Alaminos station 71-7-56, TAMU.

margin. Ischium, merus, carpus, and propodus, each with unarmed mesial and lateral faces. Propodus also with dorsal row of short setae. Carpus with small dorsodistal spine. Ischium and merus of second pereopods also each with ventral row of small tubercles or spines. Coxa with ventromesial row of setae. Anterior lobe of sternite of third pereopods weakly convex, setose, unarmed.

Fourth pereopod with elongate dactyl distinctly longer than propodal rasp; dactyl with subterminal small corneous claw ventrally in large specimens; small specimens (SL<5.0 mm) with dactyl subequal to length of propodal rasp and with terminal corneous claw (see variations, p. 77); propodal rasp with two to three usually irregular rows of ovate scales. Fifth pereopod with propodal

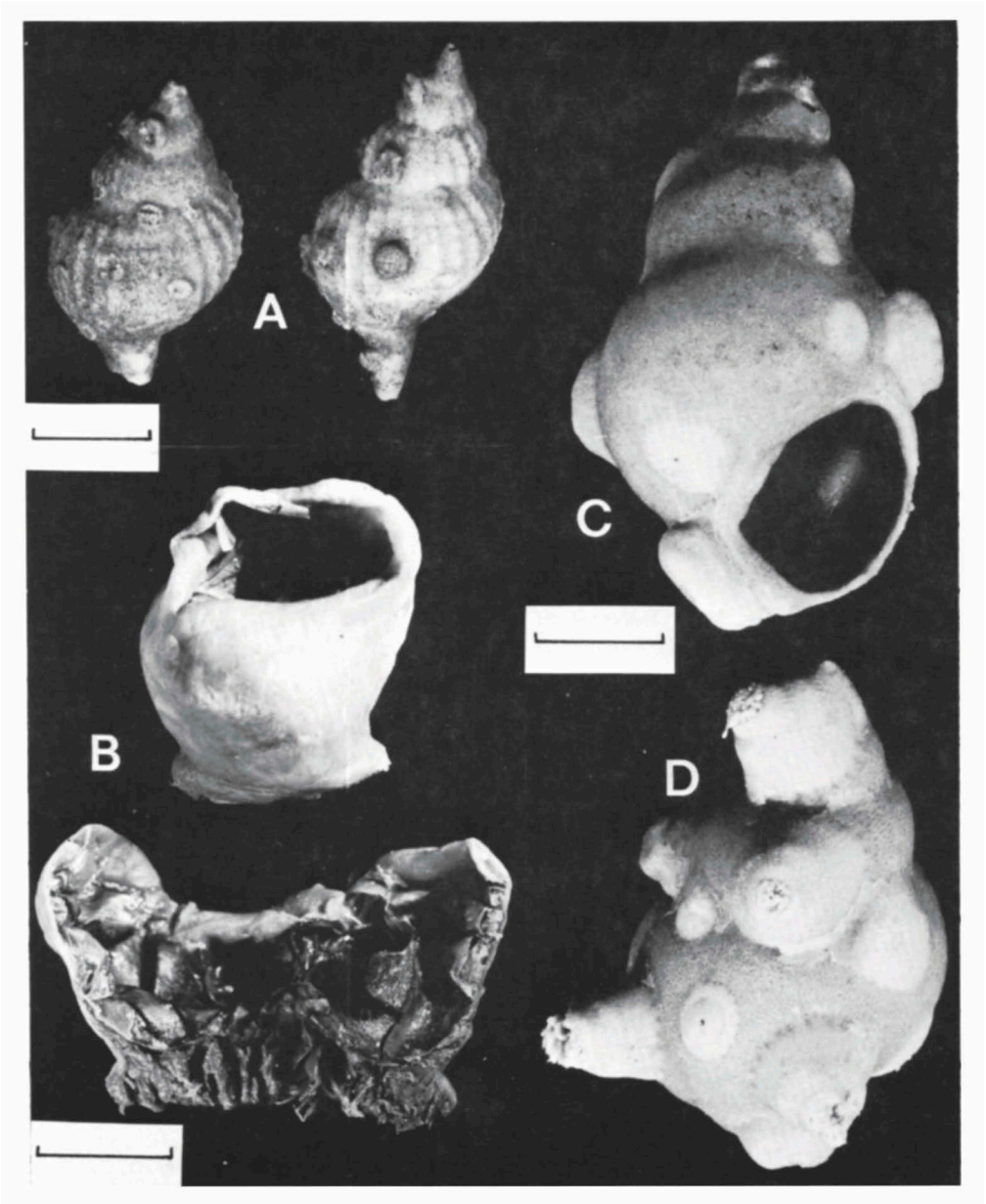

Fig. 18, examples of anthozoan symbionts of species of *Sympagurus* Smith. A, actinians on gastropod shells occupied by *S. dimorphus* (Studer); B, actinian (upper: polyp with oral portion facing down; lower: polyp with lateral wall cut longitudinally to show interior of cavity used by *S. pictus* Smith; C, *Epizoanthus* spec. [*S. dimorphus* (Studer)]; D, same. Scales equal 20 mm (A, B), and 10 mm (C, D).

rasp forming subtriangular area extending beyond midlength of propodus.

Twelve pairs of branchiae: eleven pairs of phyllobranchiae or intermediate branchiae, and one pair of vestigial pleurobranchiae; small individuals (SL<5.0) often lacking vestigial pleurobranchiae (see variations, p. 77).

Exopod of left uropod longer than broad, anterior margin broadly rounded. Telson with terminal margin separated into unequal lobes by broad, shallow, U-shaped sinus; armed with short corneous spines.

Male with paired first and second pleopods; distal lobe of first pleopod with weakly concave mesial face; second pleopod with spatulate distal segment, frequently with rudimentary exopod; small specimens (SL<5.0 mm) usually with first pleopods rudimentary or lacking, and poorly developed second pleopods. Female frequently with paired or unpaired rudimentary first pleopods; with vestigial second right pleopod.

Size. — ♂♂, SL = 3.8-17.3 mm; ♀♀, SL = 3.5-11.2 mm; ♀♀ (ovigerous), SL = 8.4-14.5 mm.

Coloration (from Smith, 1883: 39). — "In life the front part of the carapax is orange-red, bordered with white along the margin. The eye-stalks and the peduncles of the antennulae and antennae are white, except the underside of the eye-stalks, which are vermilion. The flagella of the antennulae and antennae are pale orange. A large spot of vermilion covers nearly the whole of the outer surface and extends over upon the inferior edge of the meri of the ambulatory legs, and the inferior edges of the carpi and propodi and the tips of the dactyli are marked with the same color, while the rest of the surface is white. The posterior part of the carapax and the abdomen are translucent whitish specked above with orange red, and the telson and uropods are similarly but more thickly specked with the same color. The eyes are black."

Symbiotic associations. — *S. pictus* is almost exclusively found living symbiotically with a large actinian that serves as shelter for the hermit crab (fig. 18B). The actinian produces a soft chitinous pseudo-shell or carcinoecium (Carlgren, 1928a,b), that covers the interior walls of the shelter. Verrill (1882b) described the symbiotic actinian as *Urticina consors*; subsequently (1928), he transferred the actinian to the genus *Sagartia*. Among the numerous specimens examined of *Sympagurus pictus*, only three small specimens (SL=3.3-4.9 mm) were not found inhabiting the cavity formed by this actinian.

Distribution. — Western Atlantic: from off Long Island on the northeastern coast of the United States to off French Guiana on the northeastern coast of South America. Depth range: from 180 m to 2322 m; most frequently found in depths of 200 m to 800 m.

Affinities. — This species appears to be most closely related to *S. pilimanus*. Adult specimens of the two differ considerably and are easily separated by the shape of the shield, armature and proportions of the right cheliped, shape and

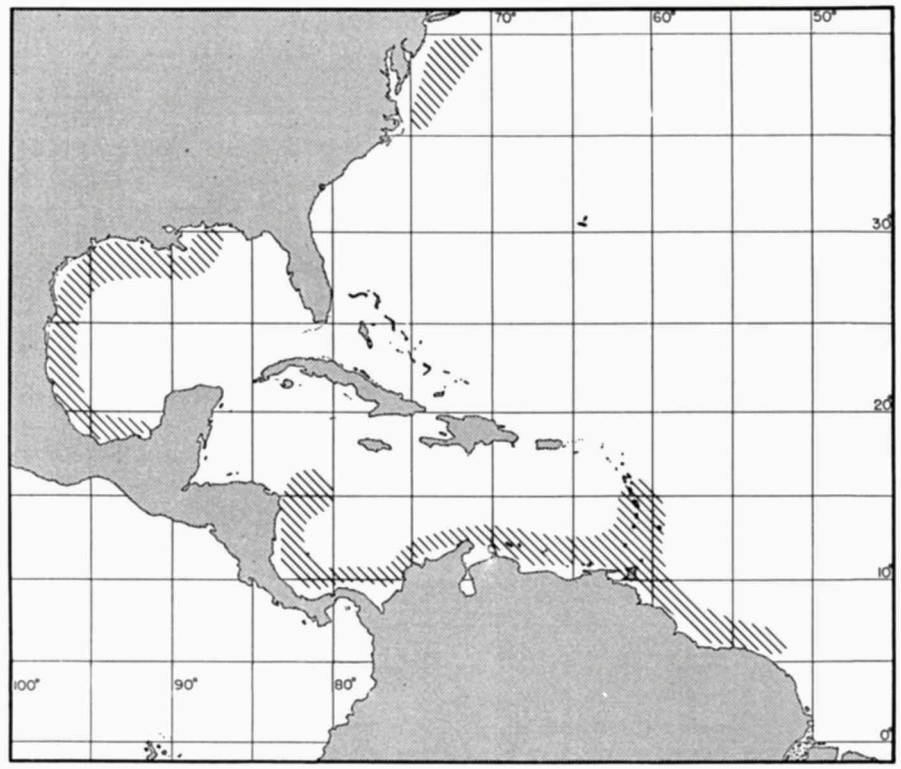

Fig. 19, map showing distribution of *Sympagurus pictus* Smith (hatched area).

length of the dactyl of the fourth pereopod, and the presence, in *S. pictus*, of vestigial pleurobranchiae. In full-grown specimens of *S. pictus*, the right cheliped is elongate (particularly in males) and armed with a few, weak spines, whereas in *S. pilimanus* the right cheliped is massive and armed with strong spines (figs. 15D,E, 20C-E). In contrast, small specimens (SL < 5.0 mm) of *S. pictus* and specimens of *S. pilimanus* of comparable size, are very similar and often hard to distinguish. Because small specimens of *S. pictus* often lack vestigial pleurobranchiae, they can easily be confused with *S. pilimanus*. This similarity is particularly evident in the right cheliped (figs. 15C, 20C); the similarity, however, disappears entirely with growth. Small specimens of the two species can be separated by the presence in *S. pictus* of a nearly straight dactyl on the fourth pereopod, a weakly asymmetrical telson, and the short rows of setae on the dorsomesial face of the dactyls of the ambulatory legs.

Remarks. — Milne Edwards' (1880) description of *Eupagurus pilimanus* was based on three specimens from the Antilles. Subsequently, Milne Edwards & Bouvier (1893) placed this taxon in *Sympagurus*; they considered,

however, that one of the specimens represented a young *S. pictus*. Although this specimen was not examined, it is clear from their description that the identification was correct. The remaining two specimens were examined and represent *S. pilimanus*. Milne Edwards' (1880) confusion of the two species can be attributed to the similarity exhibited by small individuals of the two species (see above: affinities).

Smith (1883) did not select a holotype for *S. pictus*. All of Smith's material has been examined and does represent *S. pictus*. However, because of Milne Edwards' (1880) confusion of this species with *S. pilimanus*, and the problems that might originate because of the similarities discussed above between *S. pictus* and *S. pilimanus*, a lectotype is here selected for *S. pictus*.

Sympagurus pilimanus (A. Milne Edwards, 1880) (figs. 20-23)

Eupagurus pilimanus A. Milne Edwards, 1880: 43 (in part; type locality restricted by lectotype selection: Guadeloupe, Blake station 167).

Sympagurus pilimanus: Milne Edwards & Bouvier, 1893: 63, pl. 5, figs. 8-20; Henderson, 1896: 534; Milne Edwards & Bouvier, 1897: 133; 1899: 56; Alcock, 1905: 173; Edmondson, 1925: 29; Gordan, 1956: 342; Bullis & Thompson, 1965: 10.

Parapagurus pictus: Hazlett, 1966: 88 (not *Sympagurus pictus* Smith, 1883; see remarks).

Parapagurus pilimanus: De Saint Laurent, 1972: 105.

not *Pagurus pilimanus*: A. Milne Edwards, 1884a: 176; 1884b: 27; Perrier, 1886: 301, fig. 219; Bouvier, 1888: 246; Cuénot, 1892: 56. (= *Parapagurus pilosimanus* Smith, 1879)

not *Parapagurus pilimanus*: Takeda, 1983: 104, textfig. (= *Sympagurus pictus* Smith, 1883)

Type material. — Lectotype (here selected): ♂ (SL=9.4 mm), Blake station 167, 16 09.40'N, 61 29.25'W, 315 m, 29 Jan 1879, MCZ 4013.

Material examined. — Western Atlantic: 1 ♂, Bermuda (UMML); 27 ♂♂, 20 ♀♀, Bahama Islands and Straits of Florida (UMML, USNM); 21 ♂♂, 34 ♀♀, Caribbean Sea and southwestern Atlantic (UMML, USNM, MCZ)

Description. — Shield usually as broad as long. Rostrum rounded, slightly in advance of lateral projections; with long, broad, often subdivided mid-dorsal ridge. Anterior margins weakly concave. Lateral projections broadly rounded. Anterolateral margins sloping. Lateral and posterior margins broadly rounded. Dorsal surface weakly calcified medially on posterior half, usually with numerous low blister like tubercles; with short oblique row of setae on each side of rostral ridge. Ventrolateral margins unarmed. Anterodistal margin of branchiostegite unarmed. Posterior carapace with numerous low blister like tubercles.

Ocular peduncles more than half length of shield, weakly calcified on lateral and mesial faces, with dorsal longitudinal row of setae. Corneae dilated. Ocular acicles subtriangular, terminating in strong spine; mesial margins

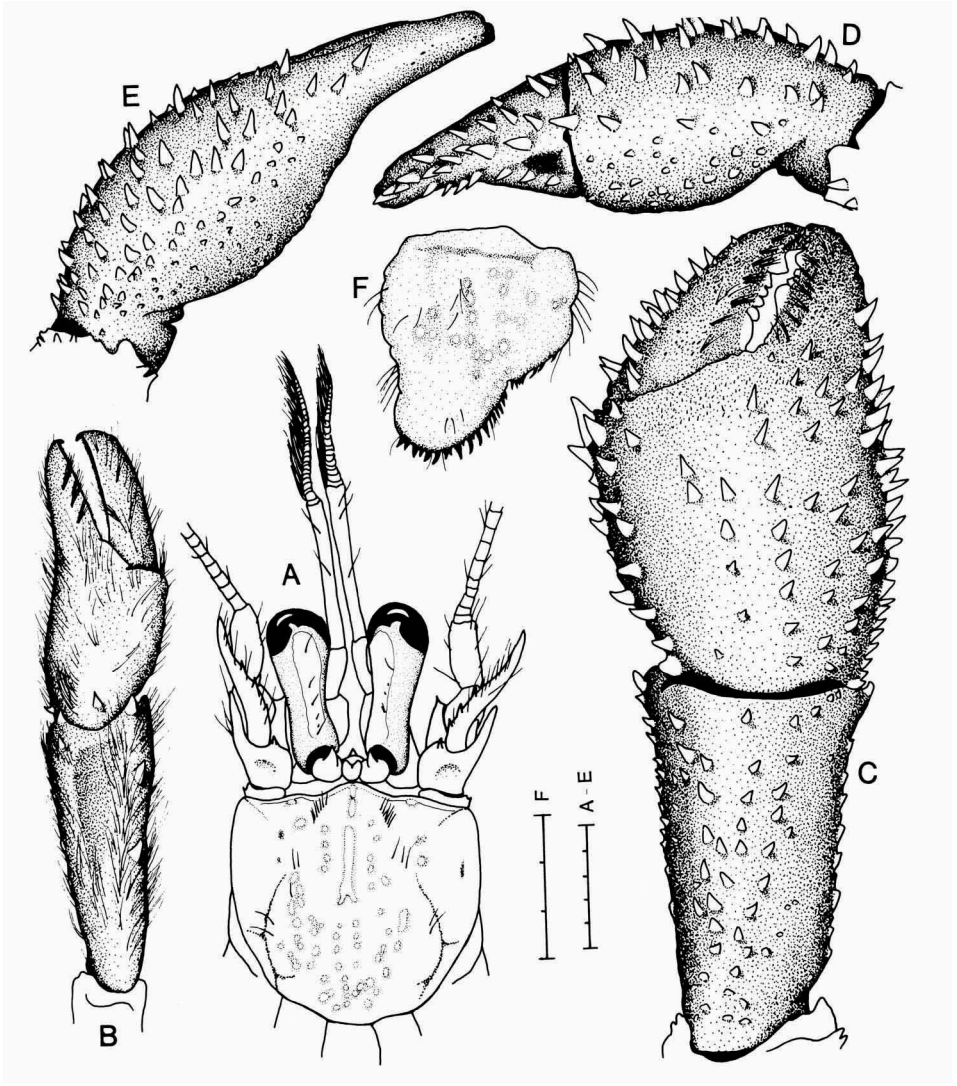

Fig. 20, *Sympagurus pilimanus* (A. Milne Edwards). Lectotype, MCZ 4013: A, shield and cephalic appendages; B, left chela and carpus; C, right chela and carpus; D, right chela (mesial view); E, right chela (lateral view); F, telson (dorsal view). Scales equal 5 mm (A-E), and 3 mm (F).

convex, lateral margins sloping; separated basally by less than basal width of one acicle.

Antennular peduncles slender, short, exceeding distal margin of corneae by less than length of ultimate segment. Ultimate segment less than twice as long as penultimate. Basal segment with strong ventromesial distal spine; lateral

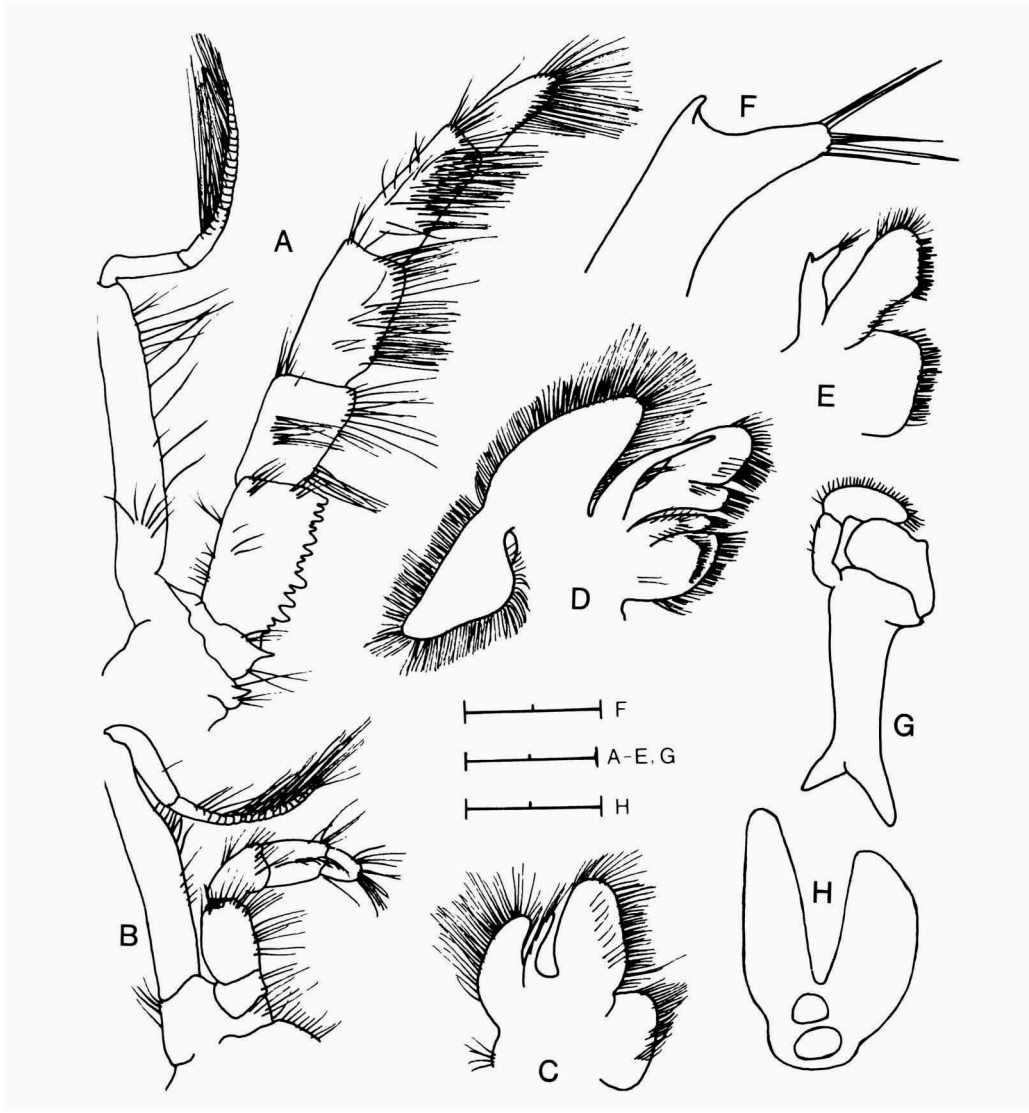

Fig. 21, *Sympagurus pilimanus* (A. Milne Edwards). ♂ (SL = 8.3 mm), Straits of Florida, Gerda station 929, UMML 32:4418: A-G, mouth parts (left, interal view): A, third maxilliped; B, second maxilliped; C, first maxilliped; D, maxilla; E, maxillule; F, endopod of same; G, mandible; H, branchia (transverse section). Scales equal 2 mm (A-E, G), 0.5 mm (F), and 1 mm (H).

face with subrectangular distal lobe with small spine, and one spine proximally.

Antennal peduncles usually not exceeding distal margin of corneae. Flagellum distinctly overreaching right cheliped; with series of two to three

long setae placed on about every ten to twenty articles, each seta being five to six flagellar articles in length. Fifth segment with row of setae mesially. Fourth segment with small spine on dorsolateral, distal angle. Third segment with strong, ventromesial, distal spine. Second segment with dorsolateral, distal angle produced, terminating in strong spine reaching to about midlength of antennal acicle; mesial margin convex, with small spine at dorsodistal angle. First segment with small spine on lateral face distally; ventromesial angle produced, with row of small spines. Antennal acicles sinuous in dorsal view, usually not exceeding distal margin of corneae; mesial margin setose, with three to four strong spines.

Mouth parts as figured (fig. 21A-G). Sternite of third maxilliped with spine on each side of midline. Epistome unarmed.

Chelipeds markedly dissimilar, covered with moderately dense or dense simple and plumose setae. Right cheliped massive. Fingers weakly curved ventromesially, each terminating in corneous claw; dorsal and ventral surface with tufts of setae; cutting edges each with several irregularly sized, calcareous teeth; cutting edge of dactyl also with distal row of small, corneous spines. Dactyl set at oblique angle to palm; with irregular rows of strong spines on mesial face. Palm with several irregular rows of weak or strong spines on dorsal surface; mesial face rounded, with irregular rows of weak or strong spines; ventromesial face with small tubercles or spines; lateral face rounded, with weak or strong spines; ventral surface unarmed or with scattered small tubercles. Carpus with irregular rows of strong spines dorsally; ventromesial and ventrolateral margins with row of spines or tubercles. Merus and ischium each with ventromesial row of strong spines. Coxa with ventromesial row of setae.

Left cheliped slender, well calcified, except occasionally on dorsolateral face of carpus. Fingers unarmed, terminating in corneous claw, with tufts of setae on dorsal and ventral surfaces; cutting edges each with row of small corneous teeth. Palm unarmed, except for proximal dorsomedian spine and lateral spine on proximal margin. Carpus and merus subtriangular. Carpus with three or more strong spines dorsally, and small spine laterally on distal margin. Merus with ventromesial and ventrolateral row of spines. Ischium with two small spines on ventromesial, distal angle. Coxa with ventromesial row of long setae.

Ambulatory legs similar from right to left, exceeding right cheliped by less than half the length of dactyl. Dactyl shorter than length of propodus, strongly curved on distal one-third, terminating in corneous claw; with dorsal row of long setae, and dorsomesial row or short rows of long setae; ventromesial margin with row of weak or strong spinules (see variations, p. 77). Ischium, merus, carpus, and propodus, each with unarmed mesial and lateral faces, and scattered low, blister-like tubercles. Carpi with one to two (rarely three) spines

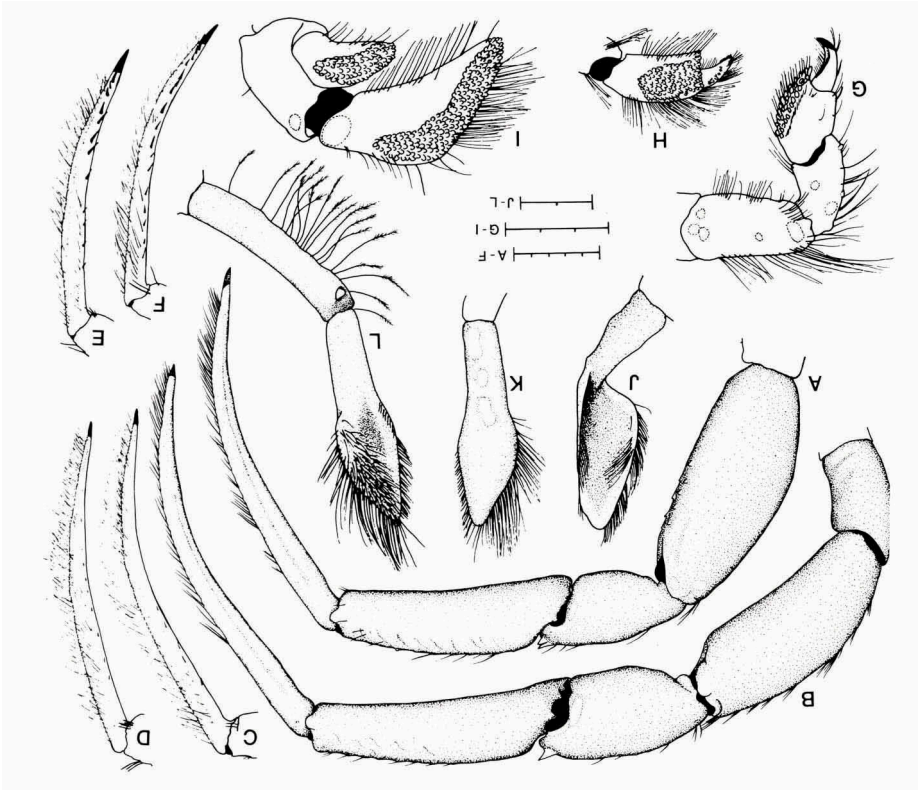

Fig. 22, *Sympagurus pilimanus* (A. Milne Edwards). A, right second pereopod (lateral view); B, right third pereopod (lateral view); C, dactyl of left third pereopod (mesial view); D, dactyl of left second pereopod (mesial view); E, dactyl of left second pereopod (mesial view); F, dactyl of left third pereopod (mesial view); G, left fourth pereopod (lateral view); H, propodus and dactyl of left fifth pereopod (lateral view); I, exopod and endopod of left uropod (dorsal view); J, male left first pleopod (mesial view); K, distal segment of male left second pleopod (posterior view); L, male second pleopod (anterior view). Scales equal 5 mm (A-F), 3 mm (G-I), and 1 mm (J-L). A-D, G-J: lectotype, MCZ 4013. E, F: ♀ (SL = 5.9 mm), Caribbean Sea, UMML 32:4414. K, L: ♂ (SL = 8.3 mm), Straits of Florida, Gerda station 929, UMML 32:4418.

on dorsodistal angle. Meri of second pereopods each with ventral row of small spines. Coxa with ventromesial row of setae. Anterior lobe of sternite of third pereopods subsemicircular, setose, armed with strong subterminal spine.

Fourth pereopod with dactyl shorter than length of propodal rasp, terminating in slender, often strongly curved, corneous claw; propodal rasp with two to three regular or irregular rows of subcircular or ovate scales; merus, carpus, and propodus each with scattered low, blister-like tubercles on lateral faces. Fifth pereopod with propodal rasp forming subrectangular area extending to midlength of propodus, or beyond it; lateral face of propodus usually with low, blister-like tubercles.

Eleven pairs of phyllobranchiae.

Uropods and telson with low, blister-like tubercles on dorsal surfaces; exopod of left uropod subtriangular. Telson with terminal margin separated by small, V-shaped sinus into strongly unequal lobes; with weak and strong, often ventrally curved, corneous spines.

Male with paired first and second pleopods; distal lobe of first pleopod with concave mesial face; second pleopod frequently with rudimentary exopod; small individuals (SL<5.0 mm) commonly with rudimentary first pleopods and poorly developed second pleopods. Female lacking first pleopods; with vestigial second right pleopod.

Size. — ♂♂, SL=2.7-14.0 mm; ♀♀, SL=3.2-11.8 mm; ♀♀ (ovigerous), SL=4.7-8.5 mm.

Symbiotic associations. — Usually found inhabiting gastropod shells without symbionts.

Distribution. — Western Atlantic: from Bermuda, the Bahamas and Straits of Florida to the southern Caribbean. Depth range: from 36 m to 2034 m; most

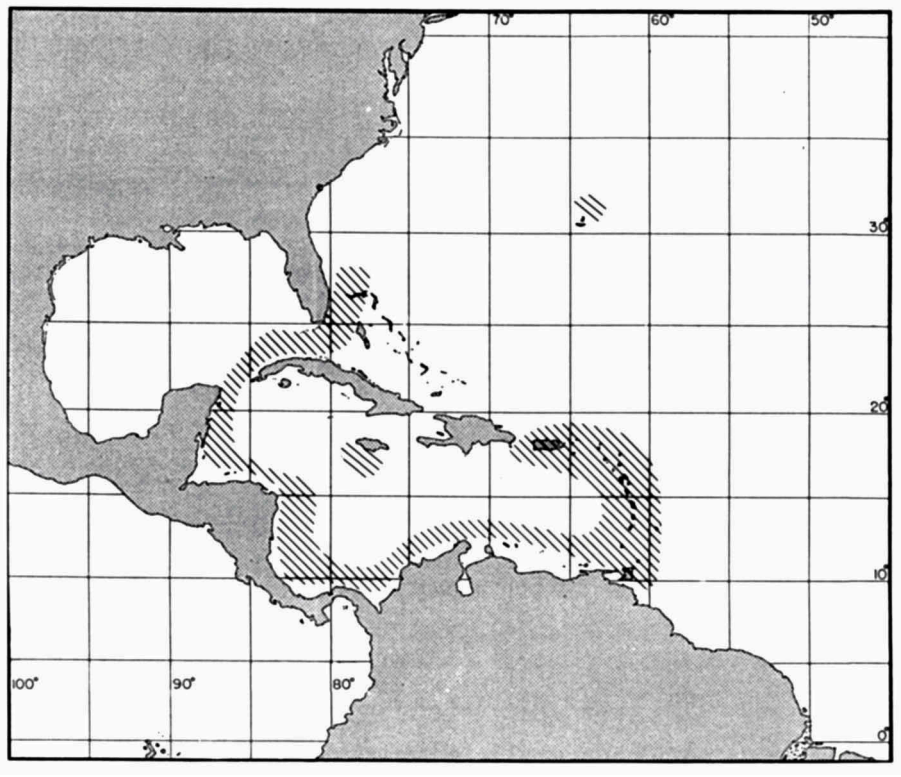

Fig. 23, map showing distribution of *Sympagurus pilimanus* (A. Milne Edwards) (hatched area).

frequently found in depths of 200 m to 600 m.

Affinities. — *S. pilimanus* is most closely allied to *S. pictus*. The relationship between the two species is inferred from the close similarity observed between small individuals of *S. pictus* and specimens of *S. pilimanus* of comparable size (see under *S. pictus*: affinities).

Remarks. — As mentioned in the remarks under *S. pictus*, Milne Edwards (1880) confounded *S. pilimanus* with *S. pictus*. Because of the possibility of confusion of the two species a lectotype is selected for this species.

In a study of behaviour of deep-water hermit crabs, Hazlett (1966) included observations on a species listed as *Parapagurus pictus*. Examination of Hazlett's specimens has shown that they actually are *S. pilimanus*.

Sympagurus acinops spec. nov.
(figs. 24-27)

Type material. — Holotype: ♂♂ (SL=5.0 mm), USNM 228519; type locality: Tongue of the Ocean (Bahama Islands), Columbus Iselin station 356, 24 23.2'N, 77 25.5'W, 1561 m, 20 Aug 1975.

Paratypes. — 60 ♂♂, 29 ♀♀, Tongue of the Ocean, Bahama Islands (RMNH, UMML, USNM).

Description. — Shield usually as broad as long. Rostrum slightly overreaching lateral projections. Anterior margins weakly concave. Lateral projections rounded. Anterolateral margins sloping. Lateral and posterior margins rounded. Dorsal surface often with several small regions of weak calcification; with longitudinal row of short setae on each side of midline, and transverse row of setae near each posterolateral angle. Ventrolateral margins usually with small spine. Anterodistal margin of branchiostegites unarmed. Posterior carapace with numerous small, low tubercles.

Ocular peduncles about half the length of shield, with dorsal, longitudinal row of setae, and usually weakly calcified on ventral surface; peduncles inflated ventrobasally. Corneae reduced, subconical, terminating in blunt to sharp, distal tip. Ocular acicles subtriangular, terminating in strong spine, separated basally by less than basal width of one acicle; mesial margins convex, lateral margins sloping.

Antennular peduncles long, exceeding distal margin of corneae by half or more than half the length of penultimate segment; with scattered setae. Ultimate segment about twice as long as penultimate. Basal segment with strong, ventromesial, simple or bifid spine; mesial face unarmed; lateral face with subrectangular, distal lobe, armed with one or more small spines, and one spine proximally.

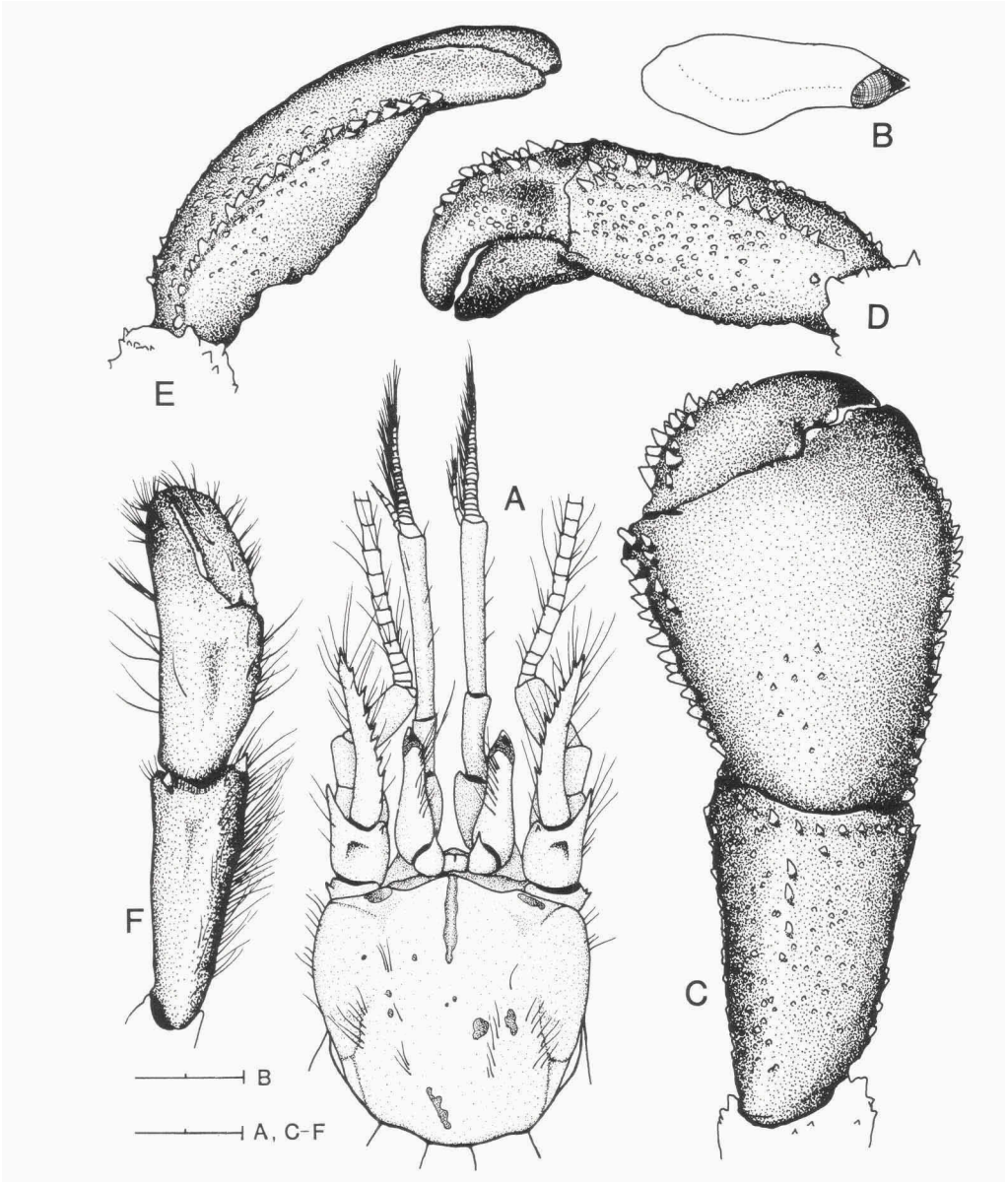

Fig. 24, *Sympagurus acinops* spec. nov. ♂ (SL = 4.7 mm), Columbus Iselin station 161, USNM: A, shield and cephalic appendages; B, eye-stalk (lateral view); C, right chela and carpus (dorsal view); D, same chela (mesial view); E, same chela (lateral view); F, left chela and carpus. Scales equal 2 mm (A, C-F), and 1 mm (B).

Antennal peduncles exceeding distal margin of corneae by slightly less than length of ultimate segment. Flagellum distinctly overreaching right cheliped,

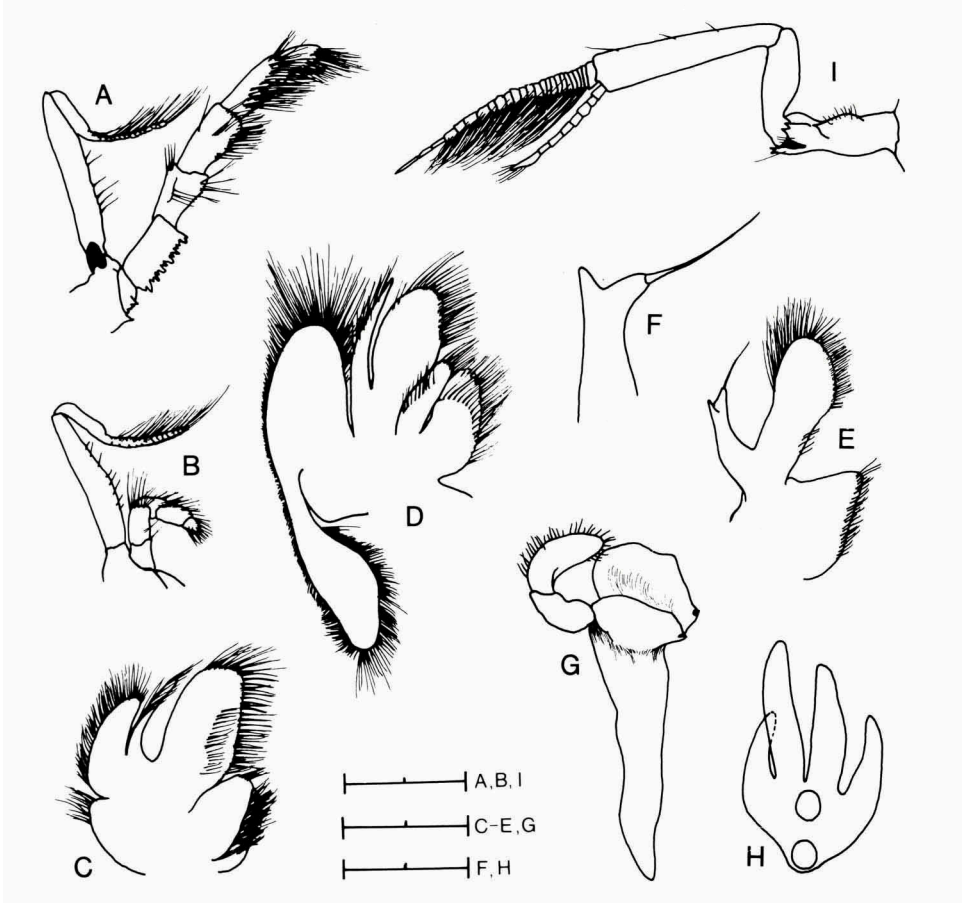

Fig. 25, *Sympagurus acinops* spec. nov. ♂ (SL = 4.6 mm), Columbus Iselin station 406, USNM: A-G, mouth parts (left, internal view): A, third maxilliped; B, second maxilliped; C, first maxilliped; D, maxilla; E, maxillule; F, endopod of same; G, mandible; H, branchia (transverse section). I, left antennule (mesial view). Scales equal 2 mm (A, B, I), 1 mm (C-E, G), and 0.5 mm (F, H).

bearing numerous setae one to four flagellar articles in length. Fifth segment with scattered setae. Fourth segment unarmed. Third segment with strong, ventromesial, distal spine. Second segment with dorsolateral, distal angle produced, terminating in strong spine; mesial margin convex, with small spine at dorsodistal angle. First segment with one to two small spines on lateral face distally; ventromesial angle produced, with one to two spines. Antennal acicles curved outwardly, exceeding distal margin of corneae by about half the length of acicle; mesial margin setose, with four to nine strong spines.

Mouth parts as figured (fig. 25A-G). Sternite of third maxilliped with spine on each side of midline. Epistomial spine, when present, short and straight.

Chelipeds markedly dissimilar, covered with moderately dense simple and plumose setae. Right cheliped massive. Fingers strongly curved ventromesially, terminating in calcareous or corneous claws; dorsal and ventral surface with tufts of setae. Dactyl set at strongly oblique angle to palm; with dorsomesial row of strong spines; cutting edge with three large, unequal, calcareous teeth, and distal row of small, corneous teeth; ventromesial face moderately concave. Fixed finger broad at base, cutting edge with two large, unequal, calcareous teeth. Palm unarmed dorsally, except for few small median spines proximally; dorsomesial margin well delimited with row of strong spines; ventromesial face rounded, with small tubercles; palm and fixed finger with well delimited dorsolateral margin, armed with strong spines; ventral surface with scattered, small tubercles. Carpus with tubercles dorsally, often with dorsomedian row of small spines; mesial face strongly sloping; dorsodistal margin with transverse row of small spines. Merus subtriangular in cross-section; dorsal surface with scattered, small tubercles; ventromesial angle rounded distally, with row of spines. Coxa with ventromesial row of long setae.

Left cheliped slender, well calcified. Fingers terminating in sharp corneous claws, with tufts of setae; cutting edges each with row of small corneous teeth. Palm unarmed except for dorsomesial row of small tubercles. Ischium, merus, and carpus, slender, subtriangular in cross-section. Carpus with long setae dorsally; with strong dorsodistal spine and small lateral spine on distal margin. Coxa with ventromesial row of long setae.

Ambulatory legs similar from right to left, overreaching right cheliped by about one-fourth the length of dactyls. Ischium, merus, carpus, and propodus, each with unarmed, mesial and lateral faces, dorsal row of long setae, and scattered setae on ventral margin. Dactyl about twice as long as propodus, more strongly curved distally than proximally, terminating in sharp corneous claw; with dorsodistal and dorsomesial distal row of long setae, and ventromesial row of widely spaced spinules. Carpus with small, dorsodistal spine. Coxa with ventromesial row of setae. Anterior lobe of sternite of third pereopods subsemicircular, setose, with small subterminal spine.

Fourth pereopod with subtriangular dactyl shorter than length of propodal rasp, terminating in corneous claw, with ventrolateral row of small, corneous spines; propodal rasp with row of ovate scales.

Fifth pereopod with dactyl usually overreaching fixed finger, with row of small scales on outer surface; propodal rasp forming subtriangular area extending to about midlength of propodus.

Twelve pairs of branchiae: eleven pairs of trichobranchiae and one pair of vestigial pleurobranchiae.

Exopod of left uropod longer than broad, anterior margin broadly rounded.

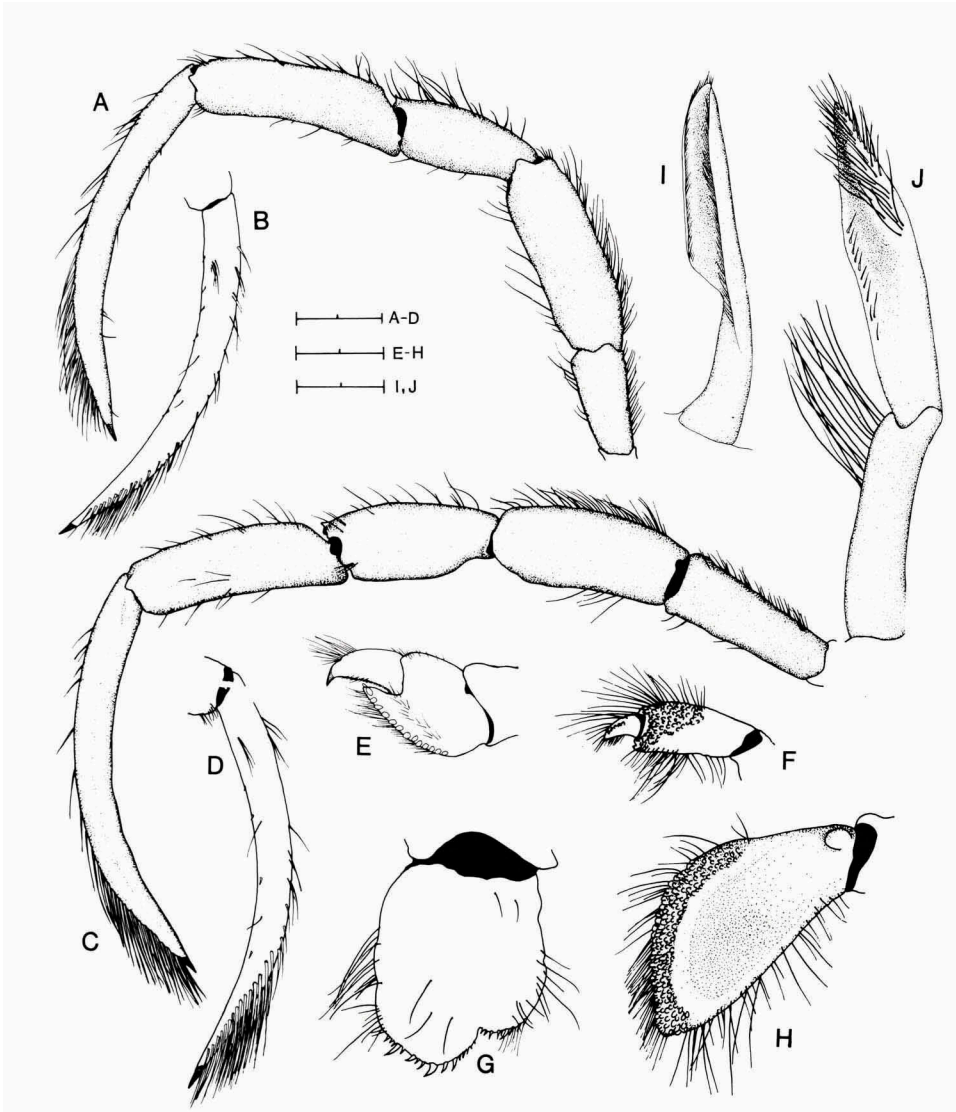

Fig. 26, *Sympagurus acinops* spec. nov. ♂ (SL = 4.7 mm), Columbus Iselin station 161, USNM: A, left second pereopod (lateral view); B, dactyl of same (mesial view); C, left third pereopod (lateral view); D, dactyl of same (mesial view); E, propodus and dactyl of fourth left pereopod (lateral view); F, propodus and dactyl of fifth left pereopod (lateral view); G, telson (dorsal view); H, exopod of left uropod (dorsal view); I, left first pleopod (mesial view); J, left second pleopod (anterior view). Scales equal 2 mm (A-D), 1 mm (E-H), and 0.5 mm (I, J).

Telson with small, low tubercles dorsally; with moderately deep V-shaped sinus separating asymmetrical lobes; terminal margin armed with weak and strong, usually curved, corneous spines.

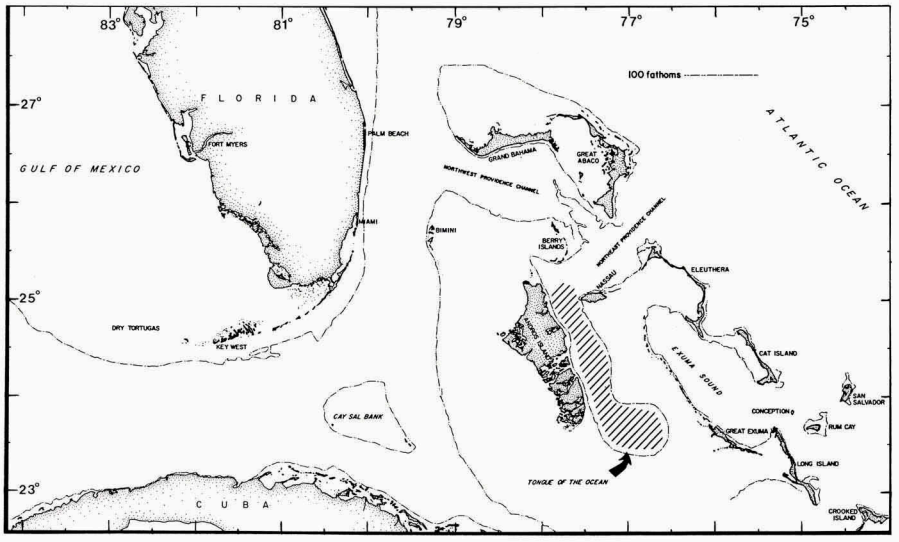

Fig. 27, map showing distribution of *Sympagurus acinops* spec. nov. (hatched area).

Male with paired, well developed first and second pleopods. Distal lobe of first pleopod elongate, subcylindrical, with row of setae on anteromesial and posteromesial margins. Distal segment of second pleopod twisted near tip; posterior face often with low tubercles. Female lacking first pleopods.

Size. — ♂♂, SL=3.0-6.5 mm; ♀♀, SL=3.3-5.6 mm; ♀♀ (ovigerous), SL=3.2-4.6 mm.

Symbiotic associations. — Usually found living without symbionts. Occasionally, individuals are found inhabiting shells with one or more small anthozoan polyps (actinians or zoanthids) attached.

Distribution. — Western Atlantic; known only from the Tongue of the Ocean, Bahama Islands. Depth range: from 1246 m to 2537 m; most frequently found in depths of 1300 m to 1400 m..

Etymology. — The specific name is derived from the Greek *akis* meaning point, and *ops* meaning eye, and refers to the shape of the corneae.

Affinities. — *S. acinops* spec. nov. is unique among the western Atlantic species in having reduced corneae that terminate in a blunt to sharp tip. *S. minutus*, from the Indo-West Pacific, has similarly shaped corneae; however, these species differ significantly in other characters, such as the shape of the epistomial spine, the telson, the exopod of the left uropod, and the branchiae. The similarity of the corneae does not necessarily indicate phylogenetic relationships between the species, as reduced eyes are more probably an ecological adaptation.

Sympagurus bicristatus (A. Milne Edwards, 1880) (figs. 28-31, 40A, B)

Eupagurus bicristatus A. Milne Edwards, 1880: 43 (in part; type locality: off Frederickstadt, Blake station 136); Bouvier, 1891a: 402; Milne Edwards & Bouvier, 1893: 154, pl. 11, figs. 11, 12; 1894a: pl. 11, legends for figs. 1-15 (see remarks).

Eupagurus? *bicristatus*: Milne Edwards & Bouvier, 1893: 155, pl. 11, legends for figs. 11, 12 (see remarks).

Sympagurus bicristatus: Milne Edwards & Bouvier, 1892b: 205; 1894a: 69, pl. 11, figs. 1-15; Bouvier, 1896: 128, fig. 11; Milne Edwards & Bouvier, 1897: 133; 1899: 56; 1900: 196; Alcock, 1905: 105; Przibram, 1905: 197; Bouvier, 1922: 21; Edmondson, 1925: 28; Bouvier, 1940: 129, fig. 86; Forest, 1954: 163; Gordan, 1956: 341; Forest, 1958: 99.

Parapagurus bicristatus: Carlgren, 1928a: 193; 1928b: 168; Forest, 1955: 100; Gordan, 1956: 338; Forest, 1958: 97; Ross, 1967: 306; Forest & De Saint Laurent, 1968: 115; Zariquiey-Alvarez, 1968: 252; De Saint Laurent, 1973: 791; Doumenc, 1975: 163.

Sympagurus bicristatus: Nobre, 1931: 203, fig. 111; 1936: 120, fig. 104.

?Species N. 3: Pike & Williamson, 1960: 540. (see remarks).

?*Sympagurus bicristatus*: Pike & Williamson, 1960: 540 (see remarks).

Parapagurus bicristatus bicristatus: De Saint Laurent, 1972: 112; Türkay, 1976: 31; Macpherson, 1983b: 476; Ingle, 1985: 764.

not *Parapagurus* (*Sympagurus*) *bicristatus*: Balss, 1911: 4 (= *Sympagurus indicus* Alcock, 1905).

not *Parapagurus bicristatus*: Balss, 1912: 98, figs. 6, 7 (= *Sympagurus indicus* Alcock, 1905); Forest, 1961: 231 [= *Sympagurus africanus* (De Saint Laurent, 1972)].

not *Sympagurus bicristatus*: Thompson, 1943: 418 (= *Sympagurus indicus* Alcock, 1905).

Type material. — Holotype: ♂ (SL=3.2 mm), Blake station 136, 17°43.10'N, 64°55.50'W, 907 m, 6 Jan 1879, MCZ 4039.

Material examined. — Western Atlantic: 1 ♂, Gulf of Mexico (USNM); 11 ♂♂, 2 ♀♀, Bahama Islands and Straits of Florida (UMML); 8 ♂♂, 4 ♀♀, Caribbean Sea and southwestern Atlantic (UMML). Eastern Atlantic: 1 ♂, 3 ♀♀ Canary Islands (RMNH); 4 ♂♂, 5 ♀♀, Cape Verde Islands (RMNH, USNM).

Description. — Shield usually as broad as long. Rostrum broadly rounded, often obsolete, with broad, mid-dorsal ridge. Anterior margins concave. Lateral projections subtriangular, slightly in advance of rostrum, each frequently terminating in small spine. Anterolateral margins sloping. Lateral and posterior margins broadly rounded. Dorsal surface usually weakly calcified on half or more of surface (see variations, p. 77), with short, oblique row of setae on each side of rostral ridge. Ventrolateral margins with small spine. Anterodistal margins of branchiostegite unarmed.

Ocular peduncles usually more than half the length of shield, weakly calcified on mesial and lateral faces, with dorsal, longitudinal row of setae. Corneae dilated. Ocular acicles subtriangular, terminating in strong spine; mesial margins straight, lateral margins sloping; separated basally by less than basal width of one acicle.

Antennular peduncles slender, short, usually exceeding distal margin of corneae by entire length of ultimate segment, with scattered setae. Ultimate segment about twice as long as penultimate. Basal segment with strong,

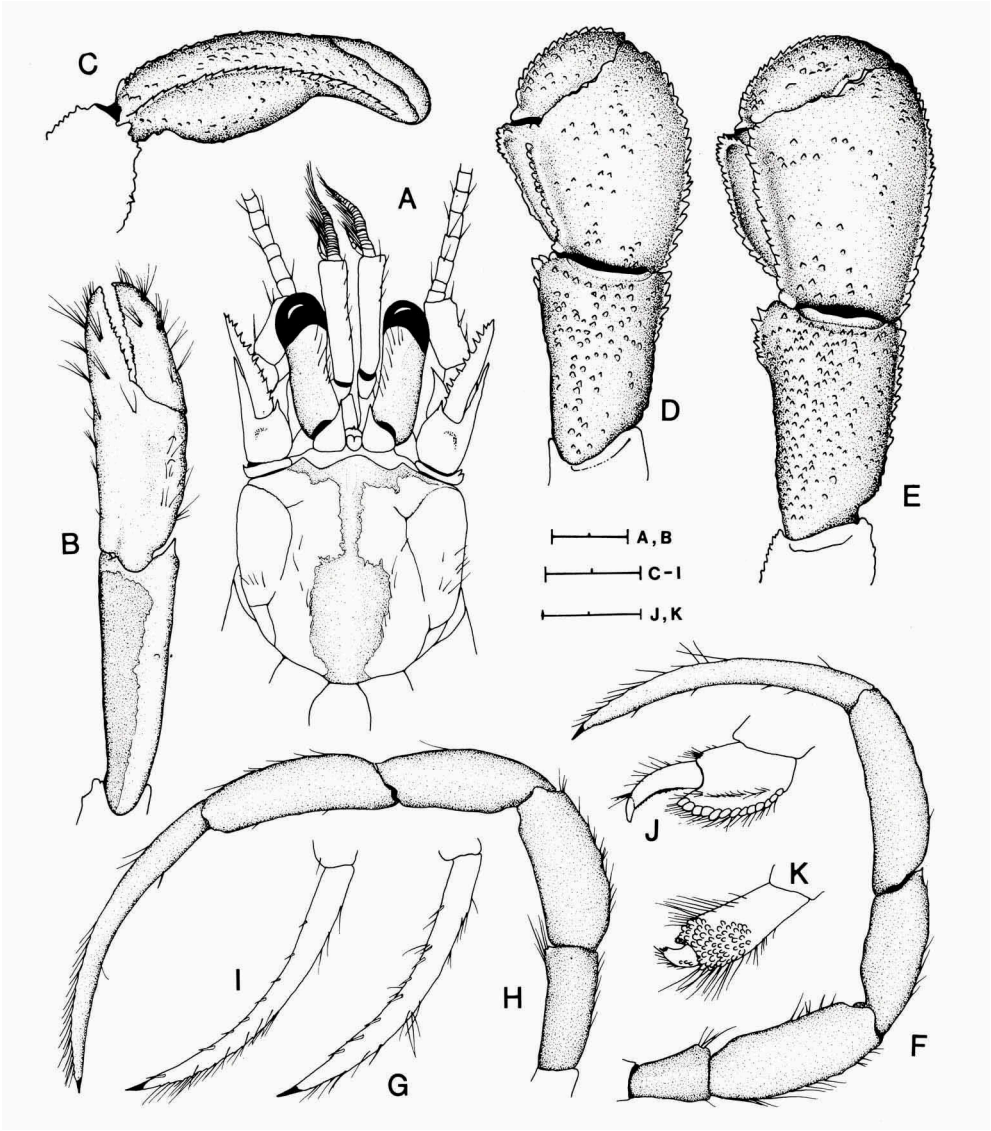

Fig. 28, *Sympagurus bicristatus* (A. Milne Edwards). A, shield and cephalic appendages; B, left chela and carpus; C, right chela (lateral view); D, right chela and carpus of female; E, right chela and carpus of male; F, left second pereopod (lateral view); G, dactyl of same (mesial view); H, left third pereopod (lateral view); I, dactyl of same (mesial view); J, propodus and dactyl of left fourth pereopod (lateral view); K, propodus and dactyl of left fifth pereopod (lateral view). Scales equal 1 mm (A, B), 2 mm (C-I), and 1 mm (J, K). A-C, E: ♂ (SL = 3.1 mm), Straits of Florida, Bellows station 78-5, USNM. D: ♀ (SL = 1.9 mm), Straits of Florida, Bellows station 78-5. USNM. F-I: ♂ (SL = 3.0 mm), Caribbean Sea, Pillsbury 589, UMML 32:4607. J, K: ♂ (SL = 4.0 mm), Gulf of Mexico, LGL Ecological Research Associates station C-3-225, USNM.

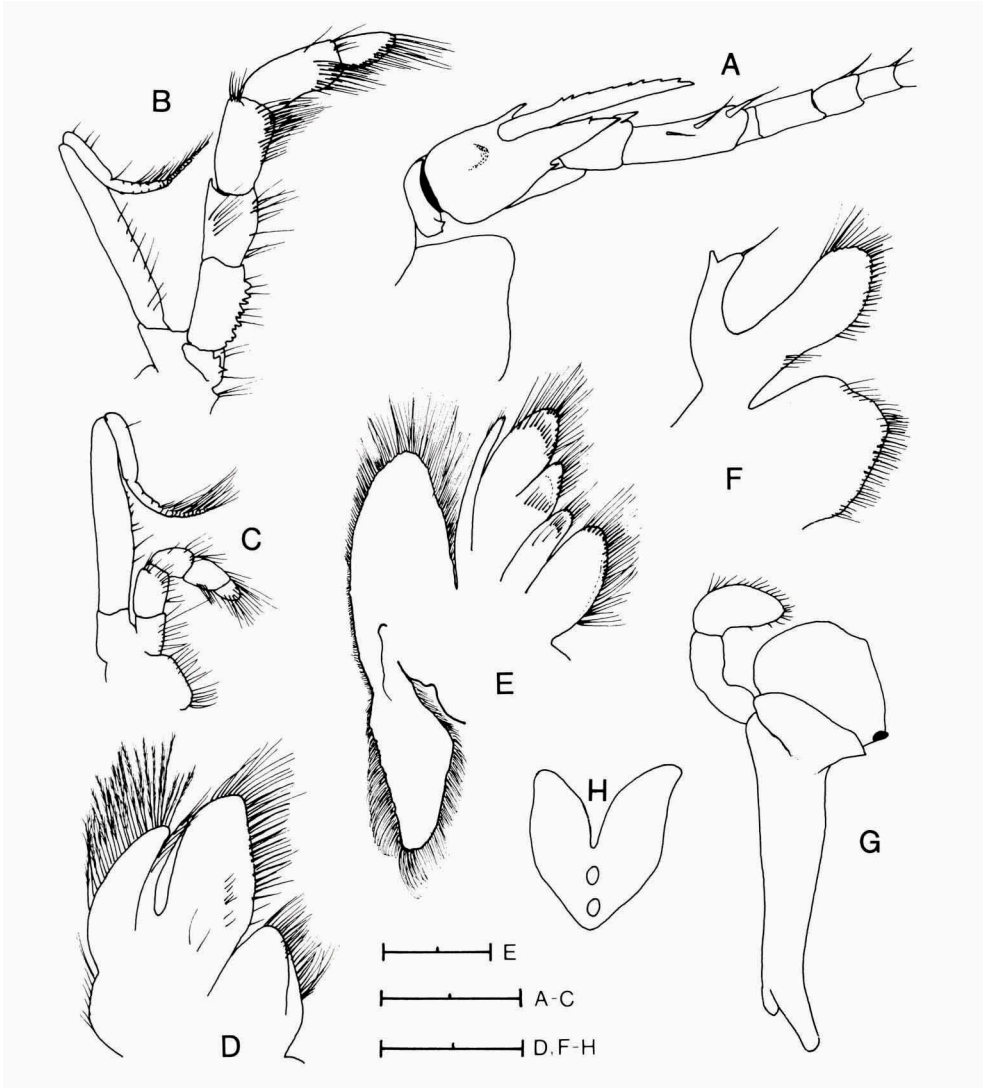

Fig. 29, *Sympagurus bicristatus* (A. Milne Edwards). A, right antennal peduncle (lateral view); B-G, mouth parts (left, internal view): B, third maxilliped; C, second maxilliped; D, first maxilliped; E, maxilla; F, maxillule; G, mandible; H, branchia (transverse section). Scales equal 1 mm (A-C), 0.5 mm (D, F-H), and 0.5 mm (E). A, H: ♂ (SL = 3.0 mm), Caribbean Sea, Pillsbury station 589, UMML 32:4607. B, G: ♂ (SL = 2.8 mm), eastern Atlantic, Talisman station 111, USNM 22917.

ventromesial, distal spine; mesial face unarmed; lateral face with subrectangular, distal lobe armed with one or more spines, and one spine proximally.

Antennal peduncles usually not exceeding distal margin of corneae. Flagellum distinctly overreaching right cheliped, with numerous setae less

than one to three flagellar articles in length. Fifth segment with row of long setae laterally. Fourth segment with small spine on dorsolateral distal angle. Third segment with strong, ventromesial, distal spine. Second segment with dorsolateral, distal, angle produced, terminating in strong, simple or multifid spine usually overreaching midlength of antennal acicle; mesial margin convex, with small spine at dorsodistal angle. First segment with one to two small spines or tubercles on lateral face distally; ventromesial angle produced, with row of small spines. Antennal acicles nearly straight in dorsal view, usually not exceeding distal margin of corneae; mesial margin setose, with ten to fourteen spines, each spine set at approximately 90° angle to longitudinal axis of acicle (at least distally).

Mouth parts as figured (fig. 29B-G). Sternite of third maxilliped with spine on each side of midline. Epistomial spine present, slender, strongly curved upward.

Chelipeds markedly dissimilar, often with iridescent areas (preserved specimens), with surfaces covered with moderately dense simple and plumose setae. Right cheliped elongate, proportions and armature strongly influenced by size and sexual dimorphism (see variations, p. 77). Fingers strongly curved ventromesially, terminating in corneous claws; cutting edges each with several irregular-sized, calcareous teeth; cutting edge of dactyl also with distal row of small corneous teeth. Dactyl set at strongly oblique angle to palm; with scattered, small tubercles or spines and tufts of setae on dorsal surface; with spines on well delimited dorsomesial margin; ventromesial face concave. Fixed finger broad at base, with tufts of setae on dorsal surface. Palm with scattered, small tubercles or spines dorsally; mesial face strongly concave, expanded distally (more so in large males; see variations, p. 77), unarmed or with scattered, small tubercles; dorsomesial and ventromesial margins well delimited, with row of spines or tubercles; dorsolateral margin well delimited, with row of spines; ventral surface unarmed or with scattered, small tubercles. Carpus with numerous, small tubercles or spines on dorsal surface; with ventromesial distal row of tubercles or spines. Merus with small tubercles on dorsal and ventral surfaces; mesial face unarmed except for ventrodistal row of spines. Coxa with ventromesial row of setae.

Left cheliped slender. Fingers terminating in corneous claw, with tufts of setae on dorsal and ventral surfaces; cutting edges each with row of small corneous teeth. Dactyl unarmed or with few small tubercles on dorsal surface proximally. Palm unarmed or with dorsomedian row of small tubercles. Merus and carpus subtriangular. Carpus weakly calcified on lateral face; with row of well spaced, small tubercles on dorsal margin, and dorsodistal spine; distal margin often with small spine laterally. Merus weakly calcified on lateral face, with ventrodistal row of small tubercles. Ischium unarmed. Coxa with ven-

tromesial row of setae.

Ambulatory legs similar from right to left, usually equalling or slightly overreaching right cheliped. Dactyl shorter than length of propodus, evenly curved throughout, terminating in corneous claw; with dorsal and dorsomesial distal row of long setae, and ventromesial row of strong spinules. Ischium, merus, carpus and propodus, each with unarmed, mesial and lateral faces, and scattered setae on dorsal margins. Carpus with small dorsodistal spine. Meri of second pereopods with one to four small spines on ventral margins distally; ventral margins of third unarmed. Ischium unarmed. Coxa with ventromesial row of setae. Anterior lobe of sternite of third pereopods subsemicircular, setose, armed with subterminal spine.

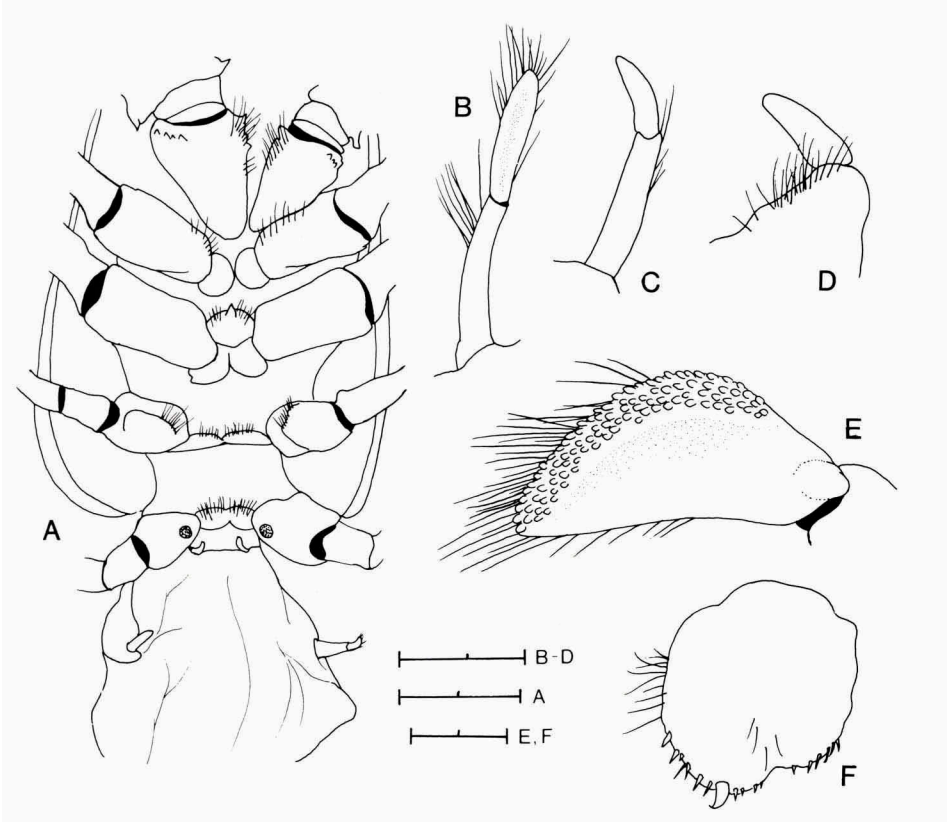

Fig. 30, *Sympagurus bicristatus* (A. Milne Edwards). A, male sternum and part of abdomen (ventral view); B, male right second pleopod (anterior view); C, male left second pleopod (anterior view); D, right second pleopod of same (lateral view); E, exopod of left uropod (dorsal view); F, telson (dorsal view). Scales equal 2 mm (A), 0.5 mm (B-D), and 1 mm (E, F). A: ♂ (SL = 4.4 mm), Straits of Florida, Gerda station 815, UMML 32:4610. B: ♂ (SL = 2.6 mm), Straits of Florida, Bellows station 78-3, USNM. C, D: ♂ (SL = 3.0 mm), Caribbean Sea, Pillsbury 589, UMML 32:4607. E, F: ♂ (SL =3.1 mm), Straits of Florida, Bellows station 78-5, USNM.

Fourth pereopod with dactyl shorter than length of propodal rasp, terminating in corneous claw, with ventrolateral row of small, corneous spines; propodal rasp with one row of ovate scales distally, often with one to two rows of ovate scales on proximal one-fourth. Fifth pereopod with dactyl often overreaching fixed finger and row of small scales on outer surface; propodal rasp forming subtriangular area extending to or beyond midlength of propodus.

Eleven pairs of phyllobranchiae.

Exopod of left uropod longer than broad, anterior margin broadly rounded. Telson with terminal margin separated by shallow, V-shaped sinus into unequal lobes; armed with weak and strong, ventrally curved, corneous spines.

Male usually with paired first and second pleopods poorly developed (see variations, p. 77). Female lacking first pleopods, with vestigial second right pleopod.

Size. — ♂♂, SL=1.3-4.4 mm; ♀♀, SL=1.8-3.2 mm; ♀♀ (ovigerous), SL=1.9-2.2 mm.

Symbiotic associations. — Usually found living in gastropod shells with one

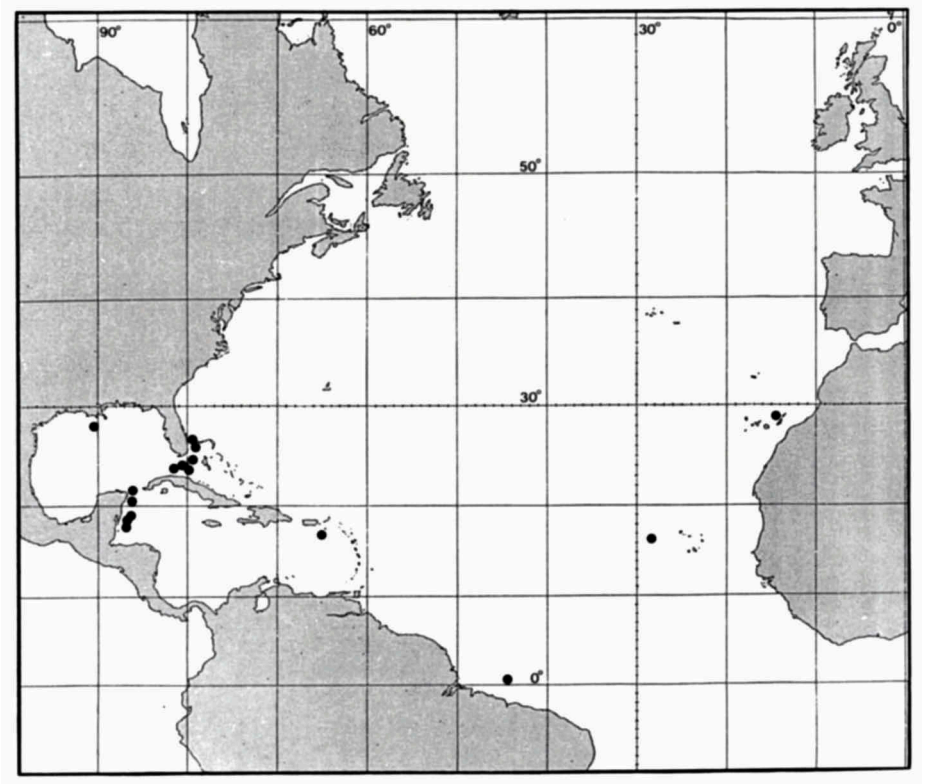

Fig. 31, map showing distribution of *Sympagurus bicristatus* (A. Milne Edwards) (solid circles).

or more anthozoan polyps (actinians or zoanthids) attached.

Distribution. — Western Atlantic: from the Straits of Florida and the Gulf of Mexico to off the coast of Maranhao, Brazil, on the northeastern coast of South America. Eastern Atlantic: Canary Islands and Cape Verde Islands. Depth range: from 270 m to 1070 m; most frequently found in depths of 400 m to 800 m.

Affinities. — This species is most closely related to *S. gracilis*. The two species can be distinguished on the basis of the mesial face of the right chela, the armature of antennal acicles, and in the case of males, the first and second pleopods (see under *S. gracilis*: affinities).

Remarks. — Following Milne Edwards' (1880) description of *Eupagurus bicristatus*, Milne Edwards & Bouvier (1892b) transferred this taxon to *Sympagurus*. However, in 1893, they again included Milne Edwards' taxon in *Eupagurus*, although they did question its generic placement in their discussion as well as in the legends for plate 11, figures 11, 12. Milne Edwards & Bouvier (1894a) definitely placed Milne Edwards' taxon in *Sympagurus*, although the name *E. bicristatus* was retained in the legend for plate 11, figures 1-15.

In a larval study, Pike & Williamson (1960) described zoeae of a species listed as "Species N. 3", and suggested that they might belong to *S. bicristatus*. Because the complete larval developmnent of parapagurid species is unknown, assignment of these zoeae to this species is questionable.

De Saint Laurent (1972) proposed three subspecies of *P. bicristatus*: *P. b. bicristatus*, *P. b. gracilis*, and *P. b. indicus*. The distinction between the typical form and the other two subspecies was based on the presence or absence of paired pleopods in the males. The study of a large series of specimens assigned to these subspecies has revealed that other differences also exist among them, and that they are distinct species. The three subspecies are here elevated to specific rank. Two of the species occur in the Atlantic, *S. bicristatus* and *S. gracilis*, and can be distinguished by the armature of the mesial face of the right chela and antennal acicles, and in the case of males, by the first and second pleopods. Contrary to De Saint Laurent's statement as to the absence of paired pleopods in males of the typical form, these can be present in *S. bicristatus* (see variations, p. 77). The third species, *S. indicus*, presumably occurs in the Indo-West Pacific.

Sympagurus gracilis (Henderson, 1888) comb. nov.
(figs. 32-35, 40C)

Eupagurus bicristatus A. Milne Edwards, 1880: 43 (in part; see remarks).
Parapagurus gracilis Henderson, 1888: 92, pl. 10, fig. 3 (type locality: off Pernambuco, Brazil,

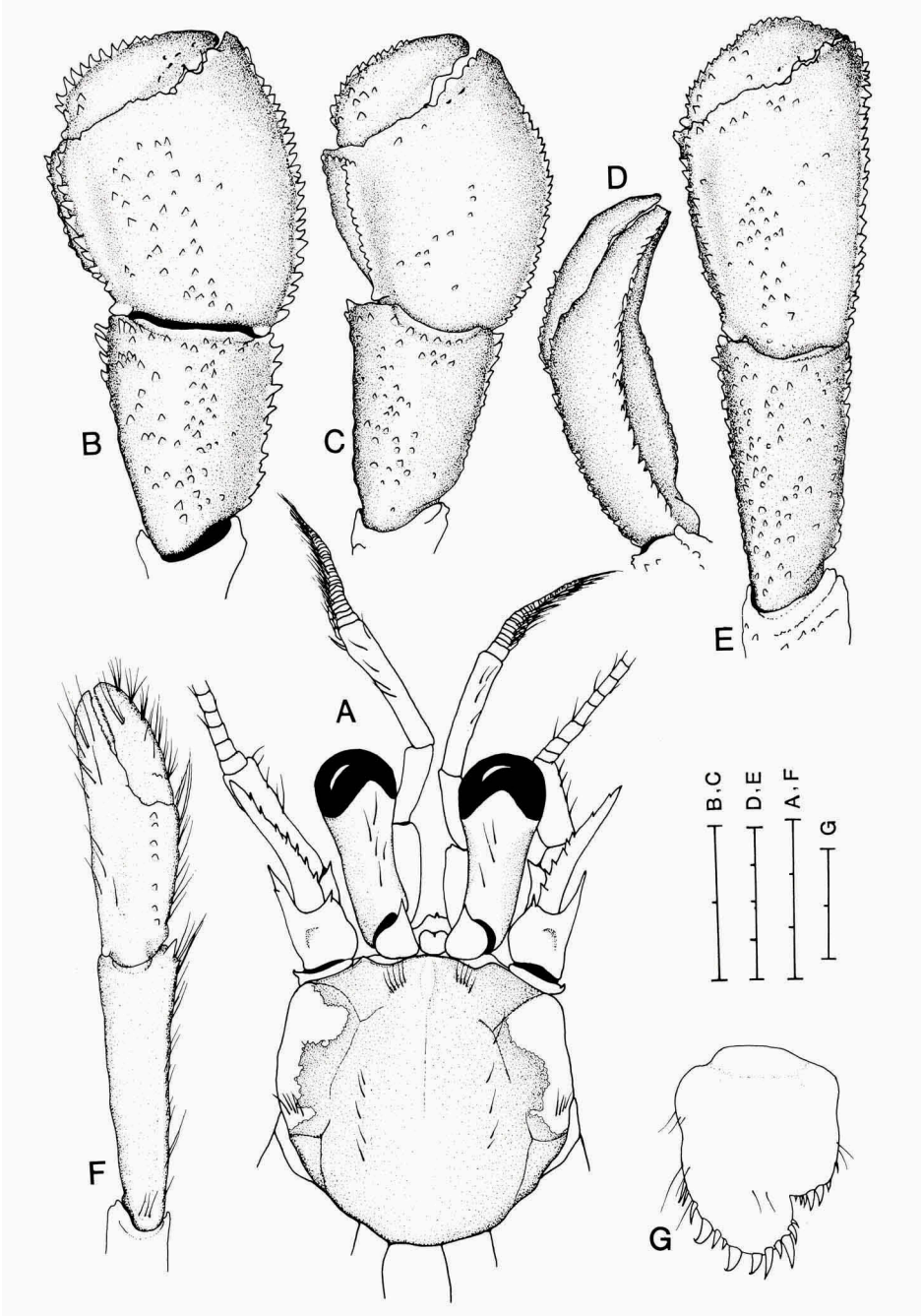

Fig. 32, *Sympagurus gracilis* (Henderson) comb. nov. A, shield and cephalic appendages; B, right chela and carpus of female; C, right chela and carpus of male; D, right chela of male (lateral view); E, right chela and carpus of same; F, left chela and carpus; G, telson (dorsal view). Scales equal 3 mm (A, F), 2 mm (B, C), 4 mm (D, E), and 1 mm (G). A: ♂ (SL = 5.5 mm), Straits of Florida, Bellows station 78-8, USNM. B: ♀ (SL = 2.7 mm), Caribbean Sea, Pillsbury station 610, UMML 32:4600. C: ♂ (SL = 2.2 mm), southwestern Atlantic, Oregon station 4226, UMML 32:4538. D-G: ♂ (SL = 4.6 mm), Caribbean Sea, Oregon station 4423, UMML 32:4591.

Challenger station 122); Murray, 1895: 359; Henderson, 1896: 534; Alcock, 1905: 172; Gordan, 1956: 338; Forest & De Saint Laurent, 1968: 114; Coelho & Araujo-Ramos, 1972: 163.

Eupagurus? bicristatus: Milne Edwards & Bouvier, 1893: 155. (see remarks).

Sympagurus arcuatus A. Milne Edwards & Bouvier, 1893: 67, pl. 5, figs. 21-28 (type locality: St. Lucia, Blake station 218); Henderson, 1896: 534; Milne Edwards & Bouvier, 1897: 133; 1899: 56; Alcock, 1905: 104; Edmondson, 1925: 28; Hale, 1941: 279; Gordan, 1956: 341; Bullis & Thompson, 1965: 10.

Parapagurus arcuatus: Balss, 1912: 89; De Saint Laurent, 1972: 108.

Pylopagurus exquisitus Boone, 1927: 71, fig. 14 (type locality: Pawnee I, north of Glover Reef, off the coast of British Honduras, 871 m); Gordan, 1956: 340. (see remarks).

Parapagurus bicristatus gracilis: De Saint Laurent, 1972: 112; Coelho & Borges Brantes dos Santos, 1980: 143.

Type material. — Lectotype (here designated): ♂ (SL=2.8 mm), Challenger station 122, 09°05'S, 34°50'W, 630 m, 10 Sep 1883, BMNH 1888: 33; Holotype of *Sympagurus arcuatus* A. Milne Edwards & Bouvier: ♀♀ (SL=2.6 mm), Blake station 218, 13°49.12'N, 61°04.40'W, 295 m, 15 Feb 1879, MCZ 6330.

Material examined. — Western Atlantic: 48 ♂♂, 33 ♀♀, Bahama Islands and Straits of Florida (MCZ, UMML, USNM); 26 ♂♂, 17 ♀♀, Caribbean Sea and southwestern Atlantic (BM, MCZ, UMML). Eastern Atlantic: 1 ♂, Gulf of Guinea (UMML).

Description. — Shield usually as broad as long. Rostrum broadly rounded, often obsolete, with broad, mid-dorsal ridge. Anterior margins concave. Lateral projections subtriangular, slightly in advance of rostrum, each frequently terminating in small spine. Anterolateral margins sloping. Lateral and posterior margins broadly rounded. Dorsal surface usually weakly calcified on half or more of surface, with short oblique row of setae on each side of rostral ridge. Ventrolateral margins with small spine. Anterolateral margin of branchiostegite unarmed.

Ocular peduncles usually more than half length of shield, weakly calcified on mesial and lateral faces, with dorsal longitudinal row of setae. Corneae dilated. Ocular acicles subtriangular, terminating in strong spine; mesial margins straight, lateral margins sloping, separated basally by less than basal width of one acicle.

Antennular peduncles slender, short, usually exceeding distal margin of corneae by nearly entire length of ultimate segment, with scattered setae. Ultimate segment about twice as long as penultimate. Basal segment with strong, ventromesial distal spine; mesial face unarmed; lateral face with subrectangular, distal lobe armed with one to two small spines, and one spine proximally.

Antennal peduncles usually not exceeding distal margin of corneae. Flagellum distinctly overreaching right cheliped; with series of two to three long setae four to eight flagellar articles in length every ten to twenty articles. Fifth and fourth segments with scattered setae. Fourth segment with small spine on dorsolateral, distal angle. Third segment with strong ventromesial distal spine. Second segment with dorsolateral, distal angle produced, termi-

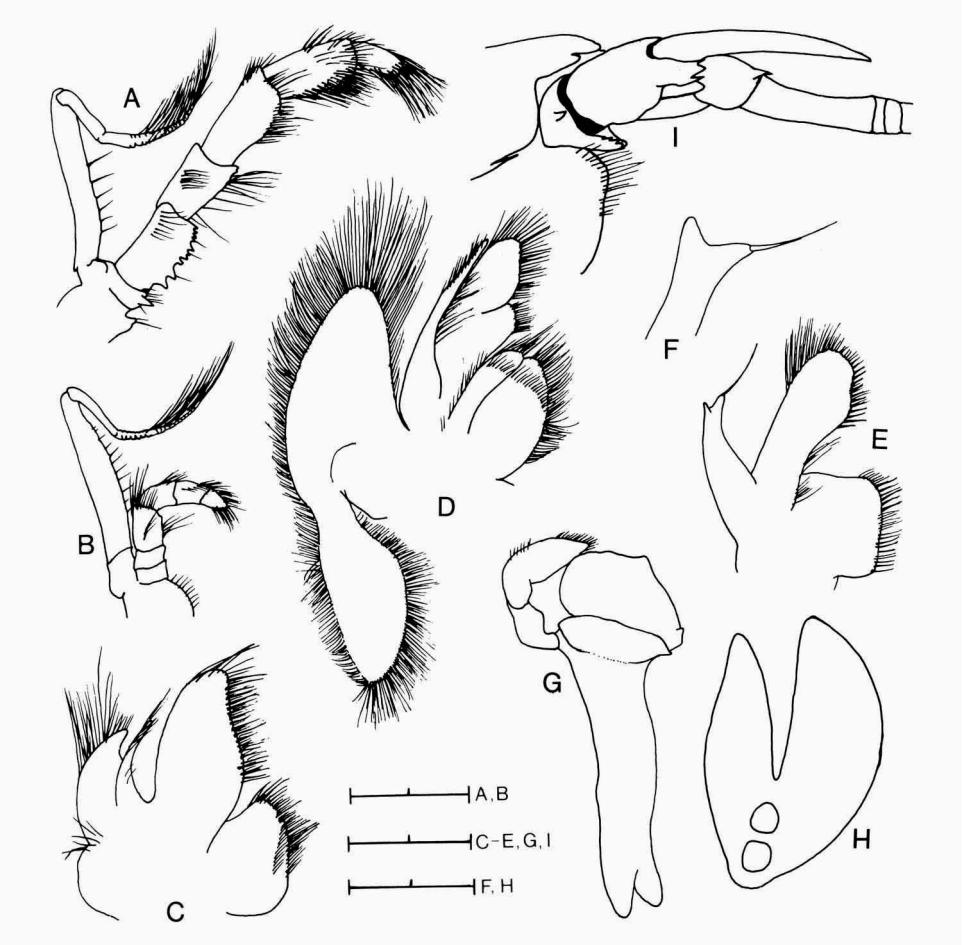

Fig. 33, *Sympagurus gracilis* (Henderson) comb. nov. A-G, mouth parts (left, internal view): A, third maxilliped; B, second maxilliped; C, first maxilliped; D, maxilla; E, maxillule; F, endopod of same; G, mandible; H, branchia (transverse section); I, right antennal peduncle (lateral view). Scales equal 2 mm (A, B), 1 mm (C-E, G, I), and 0.5 mm (F, H). A-H: ♂ (SL = 5.4 mm), Straits of Florida, Bellows station 78-4, USNM. I: lectotype, BM 1888:33.

nating in strong, simple or multifid, spine reaching to about midlength of antennal acicle; mesial margin convex, with small spine at dorsodistal angle. First segment with small spine on lateral face distally; ventromesial angle produced, with row of small spines. Antennal acicles weakly curved in dorsal view, usually not exceeding distal margin of corneae; mesial margin setose, with seven to eleven spines each set at approximately 45° angle to longitudinal axis of acicle.

Mouth parts as figured (fig. 33A-G). Sternite of third maxilliped with spine

on each side of midline. Epistomial spine invariably present, slender, strongly curved upward.

Chelipeds markedly dissimilar, often with iridescent areas (preserved specimens), with surfaces covered with moderately dense, simple and plumose setae. Right cheliped elongate, proportions and armature strongly affected by size and sexual dimorphism (see variations, p. 77). Fingers strongly curved ventromesially, terminating in corneous claws; cutting edges each with several irregular-sized, calcareous teeth; cutting edge of dactyl also with distal row of small, corneous teeth. Dactyl set at strongly oblique angle to palm, unarmed dorsally or with with scattered, small tubercles and tufts of setae; with spines on well delimited, dorsomesial margin; ventromesial face concave. Fixed finger broad at base, with tufts of setae on dorsal surface. Palm with irregular or regular, median rows of scattered, small tubercles on dorsal surface; mesial face strongly sloping, with small tubercles; dorsomesial margin well delimited, with row of tubercles or spines; ventromesial face rounded; dorsolateral margin well delimited, with row of spines; ventral surface with scattered, small tubercles. Carpus with numerous, small tubercles or spines on dorsal surface, with ventromesial, distal row of tubercles or spines. Merus with small tubercles on dorsal, lateral, and ventral surfaces; mesial face unarmed, with ventrodistal row of strong tubercles or spines. Coxa with ventromesial row of setae.

Left cheliped slender. Fingers terminating in corneous claws, with tufts of setae on dorsal and ventral surfaces; cutting edges each with row of small corneous teeth. Dactyl unarmed or with few small tubercles on dorsal surface proximally. Palm unarmed or with dorsomedian row of small tubercles or spines. Merus and carpus subtriangular. Carpus weakly calcified on lateral face, frequently with small, sharp tubercles on dorsal margin, with dorsodistal spine; distal margin often with small spine laterally. Merus weakly calcified on lateral face, with ventrodistal row of small tubercles. Ischium unarmed. Coxa with ventromesial row of setae.

Ambulatory legs similar from right to left, usually equalling or slightly overreaching right cheliped. Dactyl shorter than length of propodus, evenly curved throughout, terminating in corneous claw; with dorsal and dorsomesial distal row of long setae, and ventromesial row of weak spinules. Ischium, merus, carpus and propodus, each with unarmed, mesial and lateral faces, and scattered setae on dorsal margins. Carpus with small, dorsodistal spine. Meri of second pereopods also usually with row of small, setose tubercles or spines on dorsal margin, and one to four small spines on ventral margins distally. Coxa with ventromesial row of setae. Anterior lobe of sternite of third pereopods subsemicircular, setose, with one to two subterminal spines.

Fourth pereopod with dactyl shorter than length of propodal rasp, terminating in corneous claw, with ventrolateral row of small, corneous spines; propo-

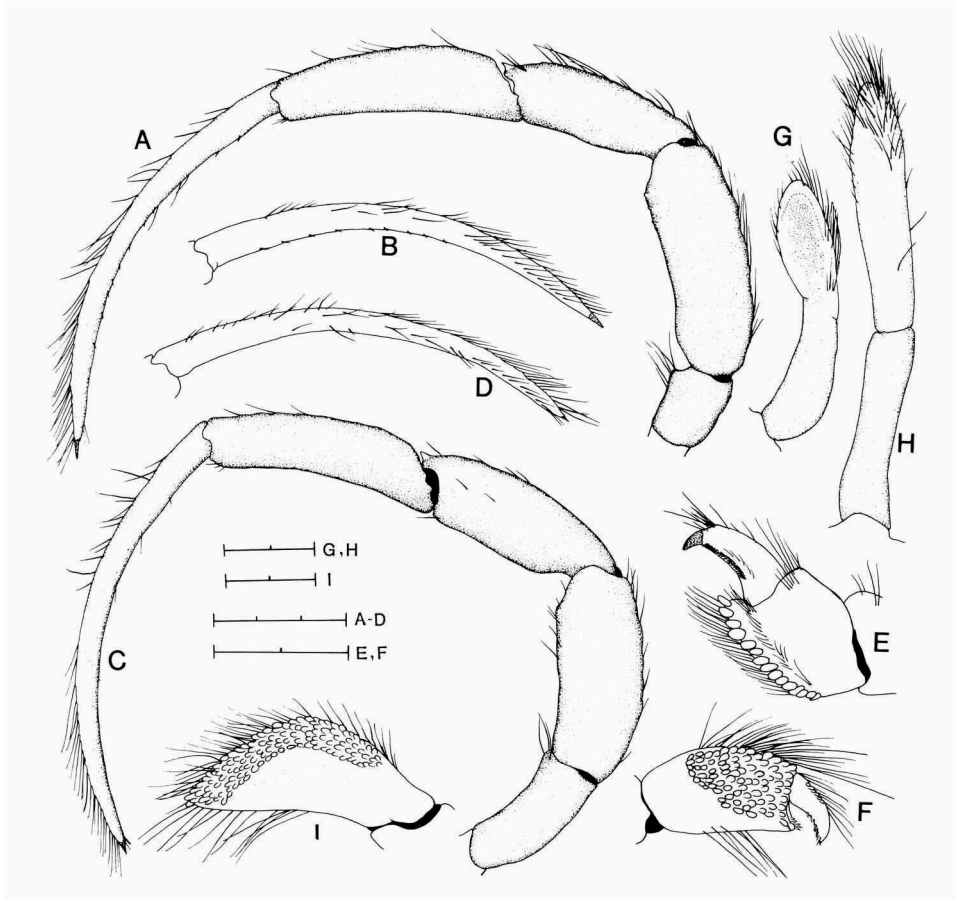

Fig. 34, *Sympagurus gracilis* (Henderson) comb. nov. A, left second pereopod (lateral view); B, dactyl of same (mesial view); C, left third pereopod (lateral view); D, dactyl of same (mesial view); E, propodus and dactyl of left fourth pereopod (lateral view); F, propodus and dactyl of left fifth pereopod (lateral view); G, male left first pleopod (mesial view); H, male left second pleopod (anterior view); I, exopod of left uropod (dorsal view). Scales equal 3 mm (A-D), 1 mm (E, F), 0.5 mm (G, H), and 1 mm (I). A-F: ♂ (SL = 4.6 mm), Caribbean Sea, Oregon station 4423, UMML 32:4591. G, H: ♂ (SL = 5.5 mm), southwestern Atlantic, Oregon station 4226, UMML 32:4538.

dal rasp with one row of ovate scales distally, with one to two rows of ovate scales on proximal one-fourth. Fifth pereopod with dactyl often overreaching fixed finger, with row of small scales on outer surface; propodal rasp forming subtriangular area extending to about midlength or more of propodus.

Eleven pairs of phyllobranchiae.

Exopod of left uropod longer than broad, anterior margin broadly rounded. Telson with terminal margin separated by V-shaped sinus into strongly unequal lobes; armed with weak and strong, ventrally curved, corneous spines.

Male with paired first and second pleopods, small individuals (SL<1.6 mm)

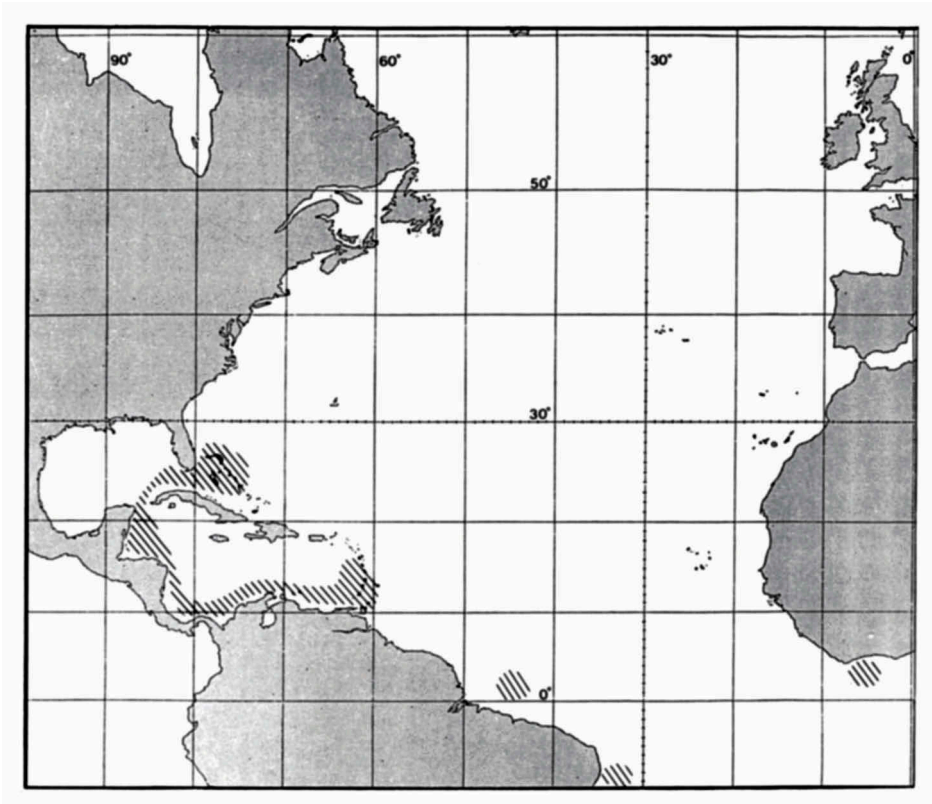

Fig. 35, map showing distribution of *Sympagurus gracilis* (Henderson) (hatched area).

often lacking first pleopods (see variations); mesial face of first pleopod weakly concave; distal segment of second pleopod spatulate. Female lacking first pleopods, with vestigial second right pleopod.

Size. — ♂♂, SL=1.8-5.5 mm; ♀♀, SL=1.0-4.0 mm; ♀♀ (ovigerous), SL=1.7-4.4 mm.

Symbiotic associations. — Usually found living in gastropod shells with one or more anthozoan polyps (actinians or zoanthids) attached.

Distribution. — Western Atlantic: from the Straits of Florida to off Pernambuco, Brazil. Eastern Atlantic: Gulf of Guinea. Depth range: from 146 m to 634 m; most frequently found in depths of 200 m to 600 m.

Affinities. — *S. gracilis* is most closely related to *S. bicristatus*. The two species can be distinguished by the characteristics of the right chela, the armature of the antennal acicles, and in males the first and second pleopods. In *S. gracilis*, the ventromesial face of the right chela is rounded, and the spines on the antennal acicles are each set at a 45° angle with the longitudinal axis of the acicle. In contrast, *S. bicristatus* has a right chela with a well delimited,

ventromesial margin, and the spines on the antennal acicle are each set at 90° angle with the longitudinal axis of the acicle. The first and second pleopods in males of *S. gracilis* are more developed than in males of *S. bicristatus* (see variations, p. 77). With these exceptions, the two species are very similar, sharing, among others, the following characters: shape and pattern of calcification of shield, an upwardly curved epistomial spine, presence of a spine on the fourth antennal segment, and phyllobranchiae.

Remarks. — Of the two specimens used by Milne Edwards (1880) for his description of *Eupagurus bicristatus*, one was later considered to represent a new species which Milne Edwards & Bouvier (1893) described as *Sympagurus arcuatus*. They indicated the transfer of the specimen to the new taxon in a footnote and cited Milne Edwards' taxon as *Eupagurus? bicristatus*. Examination of this specimen showed that it is conspecific with *S. gracilis*, thereby making *S. arcuatus* a junior synonym of *S. gracilis*.

De Saint Laurent (1972) synonymized, without comment, *Pylopagurus exquisitus* Boone with *Parapagurus arcuatus*. Although it has not been possible to examine Boone's material, it is clear, from her description and illustration, that De Saint Laurent was correct in her synonymy. Boone's taxon, therefore, is also a junior synonym of *S. gracilis*.

Henderson's (1888) description of *P. gracilis* was based on two small males from off Pernambuco, Brazil. The two syntypes were examined. Because of the poor condition of one of them, and the resulting potential for confusion with other similar species, a lectotype is here selected for *Sympagurus gracilis*.

Sympagurus dimorphus (Studer, 1883) comb. nov.
(figs. 36-38, 40E-H)

Eupagurus dimorphus Studer, 1883: 24, figs. 11, 12 (type locality: off Cape of Good Hope, South Africa, S.M.S. Gazelle, 34°13.6'S, 15°00.7'W, 211 m); Alcock, 1905: 172.

Parapagurus dimorphus: Henderson, 1888: 86, pl. 10, fig. 1; Murray, 1895: 395; Alcock, 1905: 172; Stebbing, 1910: 356; Balss, 1912: 97; Carlgren, 1923: 265, pl. 1, figs. 1, 13, 14, pl. 2, fig. 10; Balss, 1924: 768; Barnard, 1950: 452, fig. 83c,d; Haig, 1955: 18; Gordan, 1956: 338; Füller, 1958: 164; Forest & De Saint Laurent, 1968: 115, pl. 1, figs. 5, 6; Coelho & Araujo-Ramos, 1972: 164; De Saint Laurent, 1972: 108; Scelzo, 1973: 166; De Saint Laurent, 1973: 791, fig. 6; Hand, 1975: 513; Probert, Batham, & Wilson, 1979: 381; Coelho & Borges Brantos dos Santos, 1980: 143; Kensley, 1981: 33; Schembri, 1982: 860; Macpherson, 1983a: 12; 1983b: 472; Schembri & McLay, 1983: 28, fig. 6a,b.

Parapagurus brevimanus: Balss, 1911: 4, fig. 5; 1912: 100, fig. 9; Forest & De Saint Laurent, 1968: 116; De Saint Laurent, 1973: 791. (see remarks)

Sympagurus arcuatus johnstoni Hale, 1941: 279, fig. 13a-d; Gordan, 1956: 341; Forest & De Saint Laurent, 1968: 116. (see remarks).

Sympagurus arcuatus mawsoni Hale, 1941: 280, fig. 14a-c; Gordan, 1956: 341; Forest & De Saint Laurent, 1968: 116. (see remarks).

?*Parapagurus* sp. 2: De Saint Laurent-Dechancé, 1964: 15, figs. 2, 7, 11-19 (see remarks).

?Species S.A. 1: Williamson & von Levetzow, 1967: 181, figs. 2a-m, 3a-g (see remarks).
?*Parapagurus dimorphus*: Williamson & von Levetzow, 1967:184 (see remarks).
?not *Parapagurus dimorphus*: Milne Edwards & Bouvier, 1893:32 (see remarks).

Type material. — Syntypes: not examined, Museum für Naturkunde der Humboldt-Universität zu Berlin.

Material examined. — Atlantic: 48 ♂♂, 19 ♀♀, southwestern and southeastern Atlantic

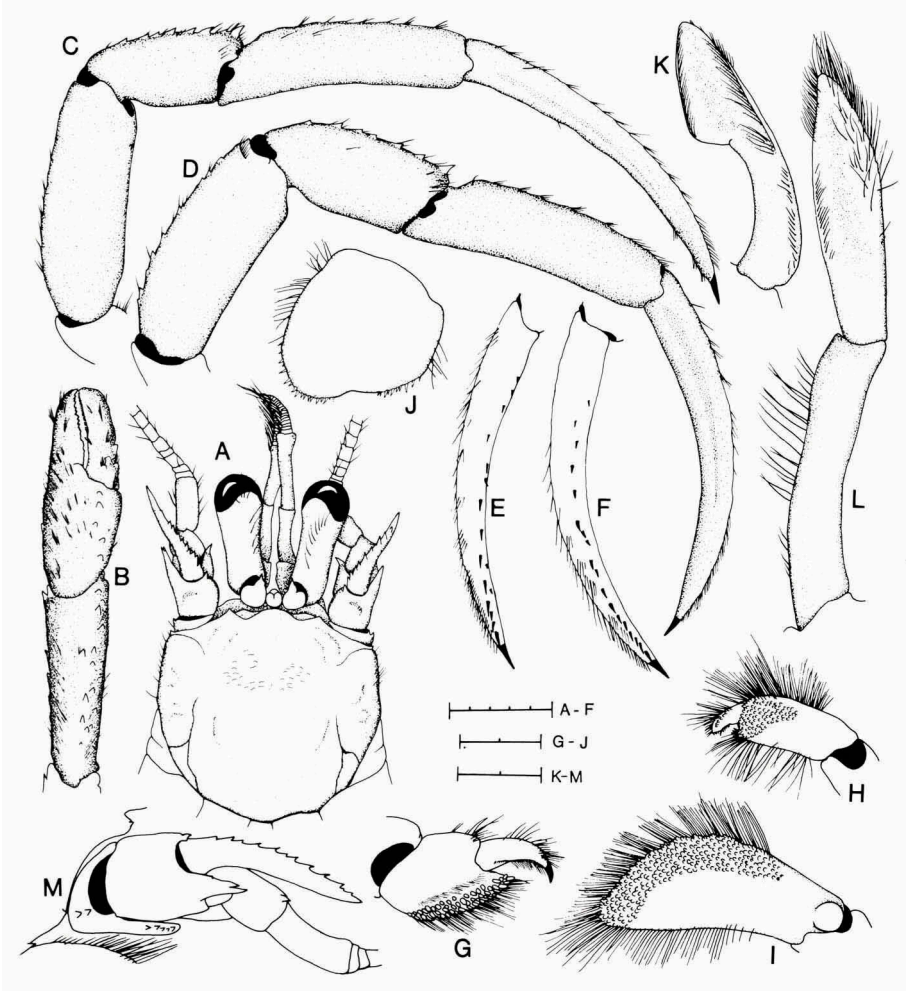

Fig. 36, *Sympagurus dimorphus* (Studer) comb. nov. ♂ (SL = 10.0 mm), Drake Passage, Eltanin station 740, USNM 155045: A, shield and cephalic appendages; B, left chela and carpus; C, right second pereopod (lateral view); D, right third pereopod (lateral view); E, dactyl of second pereopod (mesial view); F, dactyl of third pereopod (mesial view); G, propodus and dactyl of right fourth pereopod (lateral view); H, propodus and dactyl of right fifth pereopod (lateral view); I, exopod of left uropod (dorsal view); J, telson (dorsal view); K, left first pleopod (mesial view); L, left second pleopod (anterior view); M, right antennal peducle (lateral view). Scales equal 5 mm (A-F), 2 mm (G-J), and 1 mm (K-M).

(IIPB, MNHNP, SAM, USNM); 11 specimens (dry), off South Africa (SAM). Pacific: 4 ♂♂, 11 ♀♀, southeastern Pacific (USNM).

Description. — Shield usually as broad as long. Rostrum rounded, with broad mid-dorsal ridge. Anterior margins concave. Lateral projections subtriangular, with small, terminal spine. Anterolateral margins sloping. Lateral margins nearly straight, posterior margin broadly rounded. Dorsal surface often weakly calcified on medial region, with scattered setae, frequently with numerous low, blister-like tubercles. Anterodistal margin of branchiostegite unarmed. Posterior carapace with numerous low blister-like tubercles.

Ocular peduncles usually more than half the length of shield, with dorsal, longitudinal row of setae. Corneae dilated. Ocular acicles subtriangular, terminating in strong, occasionally bifid, spine; mesial margins straight, lateral margins sloping; separated basally by less than basal width of one acicle.

Antennular peduncles slender, short, distinctly exceeding distal margin of corneae. Ultimate and penultimate segments with scattered setae. Ultimate segment nearly twice as long as penultimate. Basal segment with strong, ventromesial distal spine; mesial face unarmed; lateral face with subrectangular distal lobe with small spine, and one strong spine proximally.

Antennal peduncles usually not exceeding distal margin of corneae. Flagellum distinctly overreaching right cheliped, bearing numerous setae one to two flagellar articles in length. Fifth segment with scattered setae. Fourth segment with small spine on dorsolateral distal angle. Third segment with strong ventromesial distal spine. Second segment with dorsolateral, distal angle produced, terminating in strong, multifid spine usually reaching to about midlength of antennal acicle; mesial margin convex, with small spine at dorsodistal angle. First segment with one to two small spines on lateral face distally; ventromesial angle produced, with row of small spines. Antennal acicles sinuous in dorsal view, usually not exceeding distal margin of corneae; mesial margin setose, with thirteen to nineteen strong spines.

Mouth parts as figured (fig. 37A-G). Sternite of third maxilliped with spine on each side of midline. Epistomial spine, when present, short and straight.

Chelipeds markedly dissimilar, covered with moderately dense, simple and plumose setae. Right cheliped massive, proportions and armature strongly influenced by size and sexual dimorphism (see variations, p. 77). Fingers strongly curved ventromesially, terminating in corneous claws; cutting edges each with several irregular-sized calcareous teeth; cutting edge of dactyl also with distal row of small, corneous teeth. Dactyl set at strongly oblique angle to palm; with numerous tufts of setae and small spines or tubercles on dorsal surface; dorsomesial margin well delimited, with row of spines; ventromesial face concave. Fixed finger broad at base, with numerous tufts of setae and

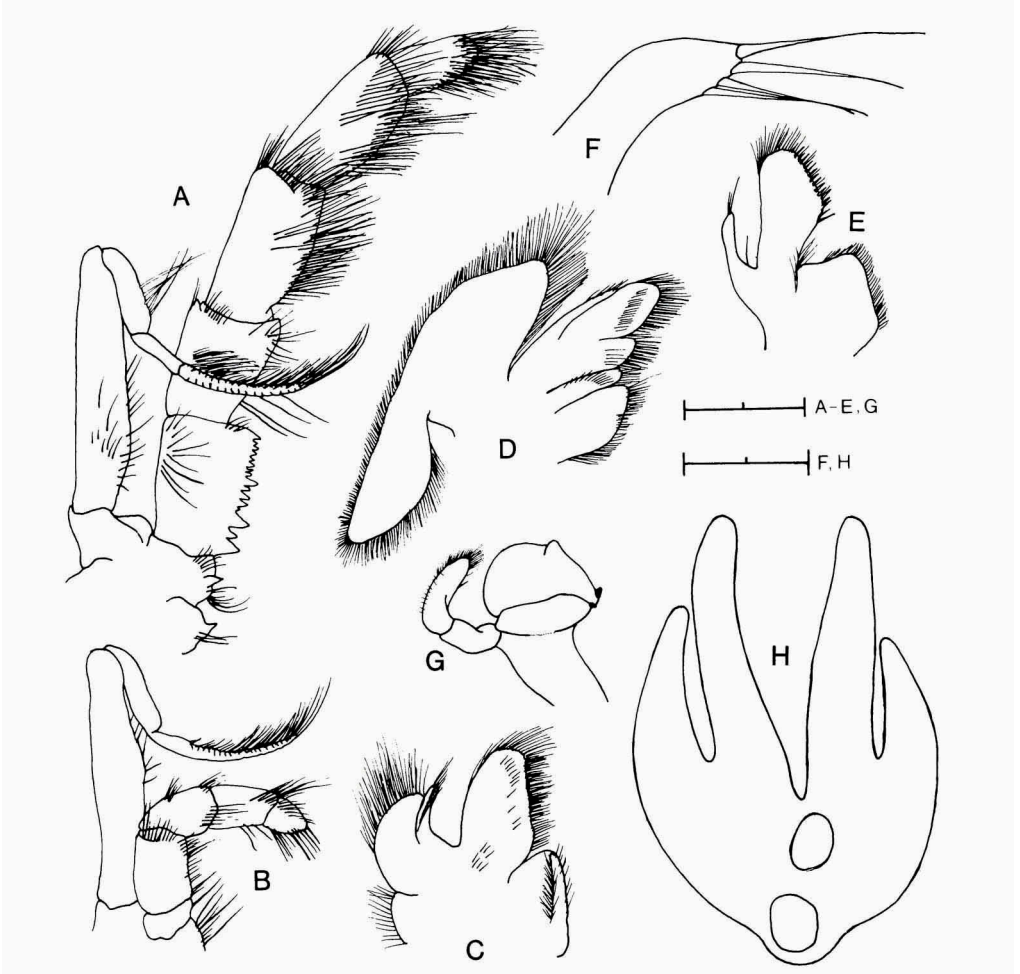

Fig. 37, *Sympagurus dimorphus* (Studer) comb. nov. ♂ (SL = 10.0 mm), Drake Passage, Eltanin station 740, USNM 155045: A-G, mouth parts (left, internal view): A, third maxilliped; B, second maxilliped; C, first maxilliped; D, maxilla; E, maxillule; F, endopod of same; G, mandible; H, branchia (transverse section). Scales equal 2 mm (A-E, G), and 0.5 mm (F, H).

small spines or tubercles on dorsal surface. Palm with numerous, small tubercles or spines on dorsal surface; mesial face strongly sloping, with small tubercles; dorsomesial margin well delimited, with row of spines; ventromesial face rounded or with well delimited, ventromesial margin; dorsolateral margin well delimited, with row of spines; ventral face with scattered, small tubercles. Carpus with numerous small tubercles and spines dorsally; dorsodistal margin with row of small spines; mesial face strongly sloping, often strongly produced distally; ventromesial margin with row of tubercles or spines; ventral surface with small tubercles. Merus with scattered, small tubercles on lateral and

ventral surfaces; mesial face unarmed; ventrolateral and ventromesial margins each with row of tubercles or spines. Ischium with ventromesial row of small tubercles. Coxa often with ventrodistal row of spines, and ventromesial row of setae.

Left cheliped slender, well calcified. Fingers with tufts of setae on dorsal and ventral surfaces, terminating in corneous claws; cutting edges each with row of small corneous teeth; cutting edge of fixed finger also with row of small calcareous teeth. Dactyl unarmed or with proximal row of tubercles dorsally. Palm with dorsomesial, dorsolateral, and often dorsomedian rows of small tubercles or spines. Carpus with row of small spines on dorsal margin; dorsodistal margin with one to two spines on lateral angle; with scattered, small tubercles on ventral surface. Merus with ventrolateral and ventromesial row of small tubercles or spines. Ischium often with ventromesial row of small tubercles. Coxa with ventromesial row of setae.

Ambulatory legs usually overreaching right cheliped by about one-fourth the length of dactyl, generally similar from right to left; armature of meri, carpi, and propodi, frequently more developed on right than left. Dactyl shorter than length of propodus, evenly curved throughout, terminating in corneous claw; with dorsal row of short setae, with several short rows of short setae dorsomesially, and ventromesial row of usually strong spinules (see variations, p. 77). Propodus usually with row of small spines dorsally. Carpus with row of spines on dorsal margin. Merus usually with ventrolateral row of small spines distally, and row of small spines dorsally. Ischium of second pereopod with small dorsodistal spine. Ischium of third pereopod unarmed. Coxa with ventromesial row of setae. Anterior lobe of sternite of third pereopods subsemicircular, setose, usually with one to three subterminal spines.

Fourth pereopod with dactyl shorter than length of propodal rasp, terminating in corneous claw, with ventrolateral row of small corneous spines; propodal rasp with three to five regular or irregular rows of ovate scales; merus, carpus and propodus each usually with scattered low, blister-like tubercles on lateral faces. Fifth pereopod with dactyl usually overreaching fixed finger, with row of small scales on outer surface; propodal rasp forming subtriangular area extending to about midlength of propodus; merus and carpus each frequently with scattered low, blister-like tubercles on lateral faces.

Twelve pairs of branchiae: eleven pairs of trichobranchiae, and one pair of vestigial pleurobranchiae.

Exopod of left uropod longer than broad, anterior margin broadly rounded. Telson frequently with scattered low, blister-like tubercles dorsally; terminal margin separated by shallow, broad, U-shaped sinus into unequal lobes; armed with short corneous spines.

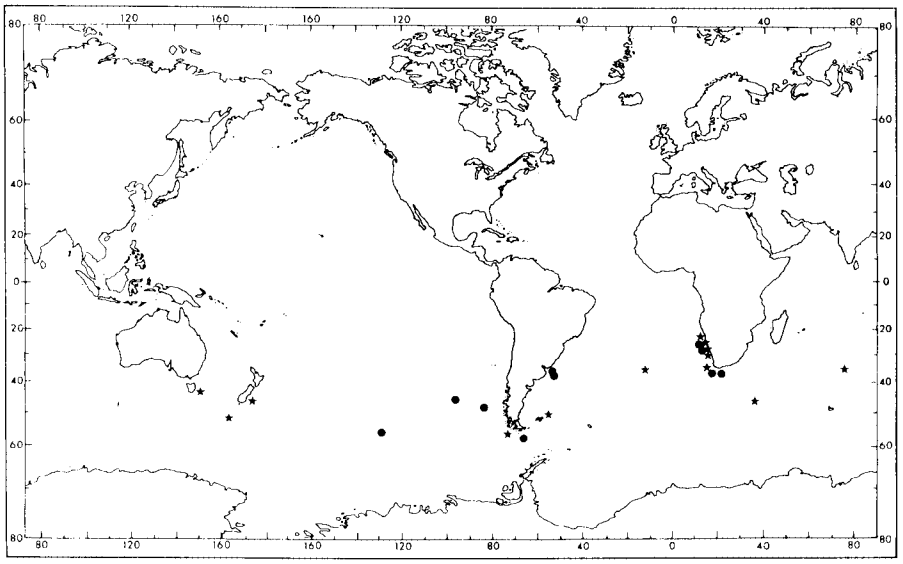

Fig. 38, map showing distribution of *Sympagurus dimorphus* (Studer). Solid circles: based on material examined; stars: based on Henderson (1888), Balss (1912), Hale (1941), Probert et al. (1979), Schembri (1982), Schembri and McLeay (1983), and Mcpherson (1983a).

Male with paired first and second pleopods; distal lobe of first pleopod with moderately concave, mesial face; distal segment of second pleopod spatulate, basal segment occasionally with short exopod. Female usually lacking first pleopods, occasionally with pair of rudimentary first pleopods (see variations, p. 77); with vestigial second right pleopod.

Size. — ♂♂, SL=3.4-16.3 mm; ♀♀, SL=5.3-12.0 mm; ♀♀ (ovigerous), SL=7.1-9.0 mm.

Symbiotic associations. — Specimens of *S. dimorphus* from the southwestern Atlantic have been found inhabiting gastropod shells with one or more anthozoan polyps (actinians or zoanthids) attached to the shells (fig. 18A). Specimens from the eastern Atlantic are commonly found living in colonies of *Epizoanthus* species (fig. 18C,D).

Distribution. — Southern hemisphere between latitudes 25° S and 57° S. Depth range: from 146 m to 603 m; most frequently found in depths of 200 m to 600 m.

Affinities. — *S. dimorphus* shares a number of characters with other species of *Sympagurus* from the western Atlantic. The presence of vestigial pleurobranchiae is shared with *S. pictus* and *S. acinops* spec. nov., and the presence of trichobranchiae is shared with *S. acinops*. Development of first and second pleopods in males of *S. dimorphus* is similar to that of *S. pilimanus*

and *S. acinops*. The general shape of the right cheliped is similar in *S. dimorphus*, *S. acinops*, *S. bicristatus*, and *S. gracilis* (e.g., the well delimited, dorsomesial and dorsolateral margins of the chela). Several other species of *Sympagurus* from the Indo-West Pacific also have a right cheliped similar to that found in *S. dimorphus*.

Remarks. — Since Studer's description, this species has been reported numerous times from the southern hemisphere in the Atlantic, Indian, and Pacific Oceans. The only southwestern Atlantic material known is that reported by Forest & De Saint Laurent (1968), and Scelzo (1973).

Milne Edwards & Bouvier (1893) questionably referred a specimen in poor condition collected off Grenada, in the Caribbean Sea, to *Parapagurus dimorphus*. The specimen was unavailable for examination, thus it has not been possible to determine its identity. *S. dimorphus* is not known at present from the northern hemisphere, and it is unlikely that Milne Edwards & Bouvier's specimen represents this species. The specimen is here questionably considered conspecific with *S. dimorphus*.

Forest & De Saint Laurent (1968) suggested that *P. brevimanus* Balss, and Hale's (1941) two subspecies of *Sympagurus arcuatus* (*S. a. johnstoni* , and *S. a. mawsoni*), were conspecific with *P. dimorphus*. Subsequently, De Saint Laurent (1972) questionably placed the taxa of Balss and Hale in synonymy with *P. dimorphus*. I have not examined Balss' and Hale's specimens, but from their descriptions and figures it would appear that their materials do represent *S. dimorphus*.

Williamson & von Levetzow (1967) indicated that the larvae of "Species S.A. 1" is most likely of *Parapagurus dimorphus*. De Saint Laurent (in Williamson & von Levetzow, 1967), concluded that her *Parapagurus* sp. 2 was the same as "Species S. A. 1". As previously mentioned, the larval development of parapagurid species is not known, and any attempt to identify the species to which the larvae belong is speculative.

MORPHOLOGICAL VARIATIONS IN WESTERN ATLANTIC SPECIES OF *SYMPAGURUS*

[The following observations apply only to the species of *Sympagurus*. A description of the morphological variation in western Atlantic species of *Parapagurus* can be found in Lemaitre (1986)].

Degree of calcification of the shield. — Various degrees of calcification have been observed. As pointed out by Lemaitre (1986), calcification can be severely altered during the preservation process, thus the possibility exists that the patterns described are artifacts of preservation. Various degrees of cal-

cification were found, however, 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. Because the calcification process of the cuticle occurs progressively during the molt cycle, it is possible that some factor may alter the process.

The surface of the shield is frequently weakly calcified in the median region. The size and frequency of occurrence of a weakly calcified region varies within species. In *S. bicristatus* and *S. gracilis*, the surface is almost always weakly calcified on more than half the surface (figs. 28A, 32A). Individuals of *S. pictus*, *S. pilimanus*, and *S. dimorphus* usually have less than half of the surface weakly calcified; in some cases, however, the entire surface is well calcified. Similar patterns of calcification have been observed in species of this genus from other areas.

Antennal peduncles. — The peduncles do not usually exceed the distal margin of the corneae in *S. pictus*, *S. pilimanus*, *S. bicristatus*, and *S. gracilis*. In *S. dimorphus*, however, the peduncle may exceed the corneae. In this species, the length by which the peduncle exceeds the corneae increases with growth. In small to medium sized individuals (SL<8.0 mm) of *S. dimorphus*, the peduncle usually does not exceed the corneae, whereas in large individuals the peduncle may exceed the corneae by as much as one-fourth the length of the ultimate segment. In *S. acinops*, the peduncle exceeds the corneae by nearly the entire length of the ultimate segment.

Epistomial Spine. — The occurrence and shape of the spine can vary in the species. In *S. pictus*, *S. dimorphus*, and *S. acinops*, a short straight spine is frequently present. The epistome in *S. pilimanus* is unarmed. In *S. gracilis* and *S. bicristatus*, the epistomial spine is invariably present in the form of a slender, upwardly curved spine; occasionally, however, specimens are found with a reduced epistomial spine, apparently the result of wear or injury.

Pilosity of the right cheliped. — Simple and plumose setae are present in the segments of the cheliped. In *S. pictus*, in particular, setation is very dense and can completely hide the armature of the cheliped like in *Parapagurus pilosimanus* (fig. 39). In other species of *Sympagurus*, setation is never quite as dense as in *S. pictus*.

Armature. — Variations in armature are largest in *S. pictus*. Small individuals (SL<4.0 mm) of this species have numerous spines on the dorsal surface of the carpus and chela. With growth, the armature is reduced to scattered, small tubercles or spines. This reduction in armature is more pronounced in males than in females (fig. 15C-E). Similar variations in armature, although less pronounced, occur in *S. bicristatus* and *S. gracilis* (figs. 28D,E, 32B-E). The shape of the mesial face of the chela in *S. bicristatus* varies with size and sex. The development of the distal portion of the mesial face can form a wing like

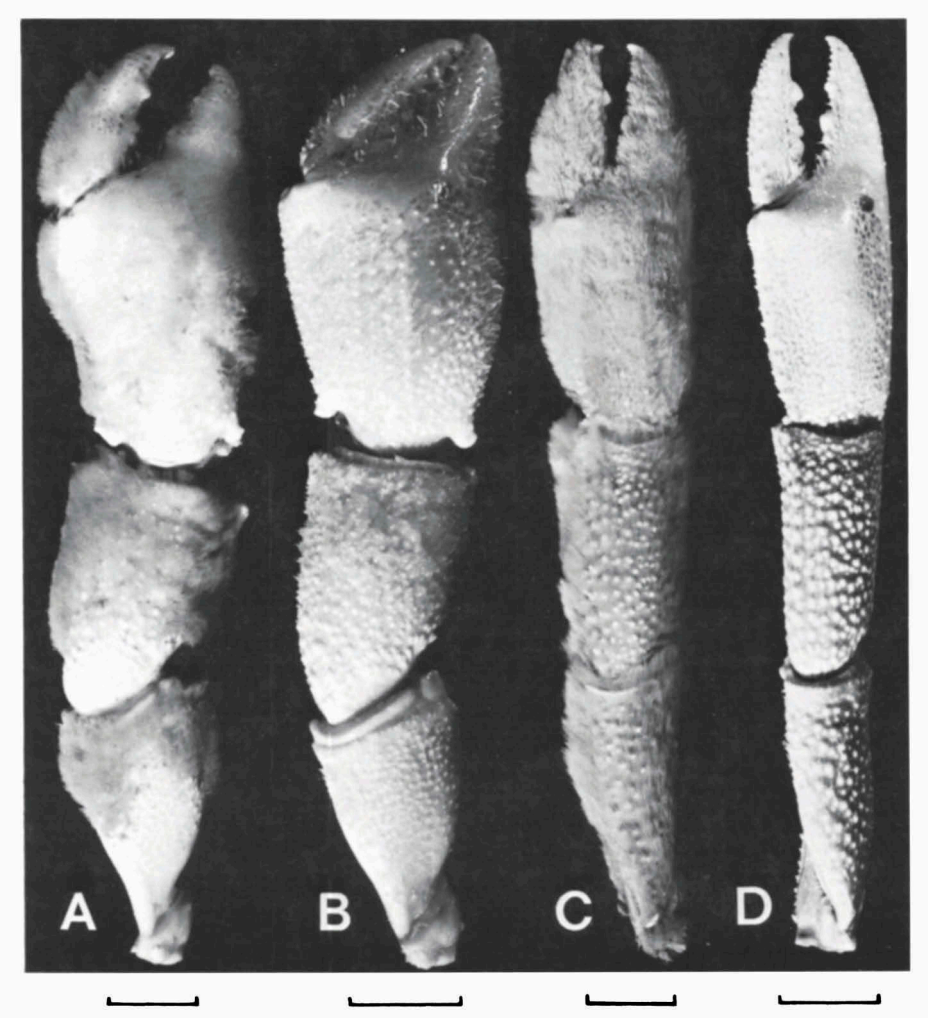

Fig. 39, right cheliped of female (B, D, setae removed). A, B, *Parapagurus pilosimanus* Smith; C, D, *Sympagurus pictus* Smith. Scales equal 5 mm (A, B), and 10 mm (C, D).

expansion in large (SL<4.0 mm) males (fig. 40A,B), which commonly have sharper spines on the margins of the chela than females. In *S. dimorphus*, the number of tubercles or spines on the cheliped increases with size (fig. 40E-H). The armature of the cheliped remains similar with growth in *S. pilimanus* and *S. acinops*.

Carpus and chela of right cheliped. — In *S. gracilis* and *S. dimorphus*, the shape of the dorsolateral margin of the chela can change from evenly convex or subsemicircular in females and males of similar size, to straight in large males (figs. 32B,C,E, 40E,G).

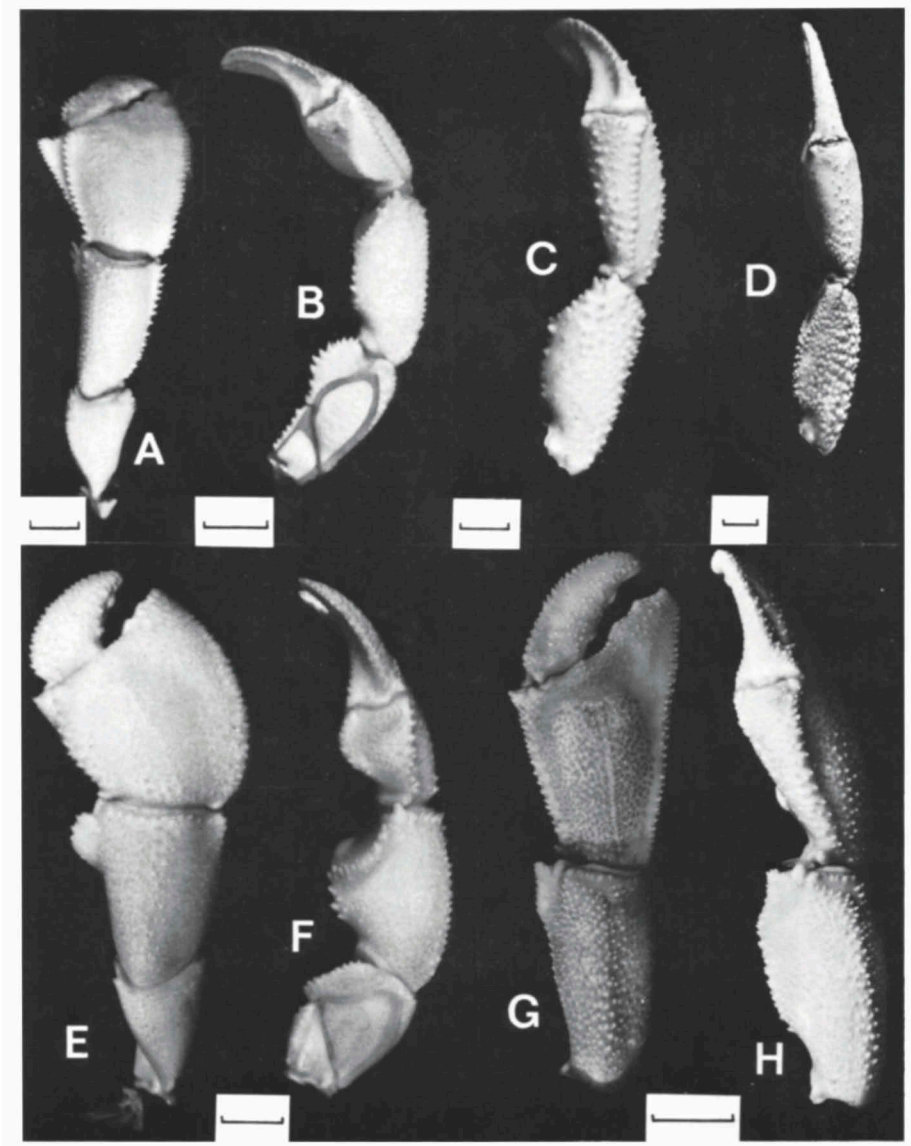

Fig. 40, right cheliped of male. A, B, *Sympagurus bicristatus* (A. Milne Edwards): A, dorsal view (SL = 4.1 mm) B, same, mesial view. C, *Sympagurus gracilis* (Henderson), mesial view of chela (SL = 5.3 mm). D, *Sympagurus pictus* Smith, mesial view of chela and carpus (SL = 15.0 mm); E-H, *Sympagurus dimorphus* (Studer): E, ♂ (SL = 10.0 mm, USNM 155045); F, mesial view of same; G, ♂ (SL = 16.3 mm), MNHNP 2496; H, mesial view of same. Scales equal 2 mm (A-C), 5 mm (D), 4 mm (E, F), and 10 mm (G, H).

Carpus of left cheliped. — The carpus is frequently weakly calcified on the lateral face, and in some cases entirely.

Dactyl of ambulatory legs (second and third pereopods). — In most species the relative length of the dactyl tends to increase with growth, and variations in armature are slight. In some species, however, changes in the characteristics of the dactyl are more pronounced. In *S. pilimanus* and *S. dimorphus*, for example, the number and strength of the spinules on the ventral margins of the dactyls can vary from a row of small, well spaced spinules (fig. 22C,D) to a row of strong spinules (figs. 22E,F, 36E,F).

Fourth pereopod. — In most species the dactyl is subtriangular and shorter than the length of the propodal rasp. In *S. pictus*, however, the shape and relative length of the dactyl changes dramatically with growth. In small specimens (SL<5.0 mm) the dactyl is subtriangular, subequal in length to the propodal rasp, and terminates in a distal claw. With growth, the dactyl becomes much longer than the propodal rasp and the claw is shifted to a subterminal position and is substantially reduced in size (fig. 17C,D).

The number of rows of scales on the propodal rasp can vary intraspecifically. The number of rows on the proximal one-third of the rasp is usually greater than the number on the distal two-thirds. The number of distal rows often can aid in identification.

Vestigial pleurobranchiae. — Vestigial pleurobranchiae are present on the last thoracic somite in *S. acinops*, *S. dimorphus*, and *S. pictus*. Small individuals (SL<5.0 mm) of *S. pictus* often lack the vestigial branchiae; however, the branchiae invariably appear with growth.

First and second pleopods. — In some species, the degree of development of the first and second pleopods in males varies considerably with growth. The first pleopods in young individuals may be lacking or present only in a rudimentary form. In males of *S. bicristatus*, paired first pleopods never develop as fully as in other species of the genus; they are, at most, represented by a short bud (fig. 30A). The second pleopods in young individuals usually are poorly developed. Young males of *S. bicristatus* may have second pleopods that are unequally sized, and often one of the pleopods is unsegmented (fig. 30C,D). Although second pleopods in species of *Sympagurus* usually lack an exopod, a short exopod is often present in males of *S. pictus* and *S. dimorphus*. Though females typically lack first pleopods, it is not uncommon to find female specimens of *S. pictus* and *S. dimorphus* with paired or unpaired rudimentary first pleopods. In females of all species, the second left pleopod has crossed rami, and a vestigial second right pleopod is present.

Third to fifth pleopods. — Males have unpaired third to fifth left pleopods each with unequal rami. Females have unpaired third to fourth pleopods each with crossed rami; the rami of the unpaired fifth pleopod are unequal and not crossed.

Terminal margin of telson. — The lobes of the terminal margin of the telson

are separated by a V-shaped or U-shaped sinus. The lobes are strongly asymmetrical in *S. pilimanus* and *S. gracilis*, but weakly to moderately asymmetrical in the remaining species. In *S. acinops*, *S. bicristatus*, *S. gracilis*, and *S. pilimanus*, the armature of the left lobe usually includes several strong, ventrally curved spines.

DISCUSSION

As discussed by Lemaitre (1986), the systematic confusion that has long existed among the taxa of *Parapagurus* (sensu De Saint Laurent) has resulted largely from the lack of understanding of the morphological variation exhibited by the species, and from the use of characters strongly affected by such variation (e.g., characters derived from the right cheliped). Several new or relatively new characters in structures such as the branchiostegite, antennal acicle, left cheliped, propodal rasp of fourth pereopod, exopod of left uropod, and telson, were shown by Lemaitre to be essential in distinguishing the four western Atlantic species of *Parapagurus* Smith. In reinstating *Sympagurus* and studying the western Atlantic species of this genus, several characters have proved diagnostic. These characters should also be useful in the evaluation of *Sympagurus* species from other regions. A list of these characters is included in Table 2. In species of *Sympagurus*, the right cheliped is also affected in its proportions and armature by size and sexual dimorphism. The diagnostic use of characters of this appendage in species of this genus is limited. However, in species such as *S. bicristatus* and *S. gracilis*, characters of the right cheliped (e.g., shape and armature of the right chela), do have diagnostic importance.

The genus *Sympagurus*, as defined in this paper, includes more than half of the species in the family Parapaguridae, most of which are distributed in the Indo-Pacific region. The majority of the Indo-Pacific species, however, is poorly known and it appears that the genus may still be heterogeneous. At least one character, viz., the presence of a curved epistomial spine, may be of phylogenetic significance in evaluating this genus. A curved epistomial spine is present in at least nine species: *S. africanus, S. bicristatus, S. boletifer, S. gracilis, S. indicus, S. minutus, S. monstrosus, S. orientalis,* and *S. haigae*. However, in order to ascertain any relationship among these species, other characters must be investigated as well.

As mentioned in the section on morphological variation, the development of the first and second pleopods can vary greatly with growth in males of some of the western Atlantic species of *Sympagurus*. In males of species from other regions, the first pleopods may be lacking and the second pleopods may only be developed, at most, to a rudimentary form (e.g., *S. hobbiti* and *S.*

Structure	Character
Shield	1. degree of calcification
	2. shape of rostrum, lateral projections, and posterior margin
	3. armature of ventrolateral margins of shield
	4. presence of blister-like tubercles
Ocular Peduncles and Acicles	5. degree of calcification of ocular peduncles
	6. size and shape of corneae
	7. shape and armature of ocular acicle
Antennal Peduncles and Acicles	8. relative length of peduncle and acicle
	9. armature of fourth segment
	10. armature of acicle
Epistomial Spine	11. curvature
Right Cheliped	12. armature
	13. shape of ventromesial face of dactyl
	14. shape of lateral and mesial face of chela
Ambulatory Legs	15. armature and setation of segments
Fourth Pereopod	16. shape of dactyl
	17. shape and number of rows of scales on propodal rasp
Fifth pereopod	18. length of dactyl relative to fixed finger
	19. shape of area formed by propodal rasp
Branchiae	20. type and number
Abdomen	Males
	21. shape and development of 1st and 2nd pleopods
	Females
	22. presence of rudimentary pleopods
Uropods and Telson	23. shape of exopod of left uropod
	24. shape and armature of telson

Table 2. Characters for diagnostic evaluation of species of *Sympagurus* Smith, 1883.

rutícheles). It appears that the evolutionary development or loss of the first and second pleopods in males is still at an incomplete stage in some species of this genus.

Several species of *Sympagurus* from the western Atlantic as well as from other regions have a pair of vestigial pleurobranchiae. This type of branchiae, which has also been reported by De Saint Laurent (1972), is unique among paguroids.

The presence of vestigial or rudimentary first pleopods in females has not been previously reported in species of *Parapagurus* or *Sympagurus*. The

occurrence of these pleopods in females of some species might be interpreted as a possible case of protandry. The first pleopods presumably would represent evidence of a previous male stage. However, other types of evidence usually found in protandric decapod crustaceans have not been observed (e.g., strong deviations from a 1:1 sex ratio; smaller size classes dominated by males and larger size classes dominated by females). Protandry is not known to occur in paguroids. Rather, the presence of first pleopods in females of some species appears to be another case of intraspecific variation in the occurrence of these pleopods. A similar intraspecific variation of pleopods has been reported for species of *Tomopagurus* A. Milne Edwards & Bouvier, 1893, by McLaughlin (1981).

A vestigial second right pleopod has been observed in females of the majority of species of *Sympagurus*. Females of one eastern Atlantic species, *S. rutricheles*, lack the second right pleopod. In female specimens of some species, the second right pleopod is often absent, although a scar is visible on the normal place of attachment. It thus appears that this pleopod may easily become detached (accidentally?).

The phylogenetic analysis of the species and genera of the family Parapaguridae is hindered by the lack of knowledge of the species from regions other than the western Atlantic. With the present information on the western Atlantic species, however, an evaluation of the remaining species should now be possible. Only when all species become known in sufficient detail will it be possible to investigate their phylogenetic relationships.

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APPENDIX

The following list contains the data for the stations from which specimens were collected. The information has been extracted from published accounts or official reports on the cruises and expeditions, and from museum or institution files. In cases where a depth range was given, the greatest depth is listed. The species found at each station are indicated by a number under the last column: 1, *Parapagurus pilosimanus*; 2, *P. alaminos*; 3, *P. nudus*; 4, *P. abyssorum*; 5, *Sympagurus pictus*; 6, *S. pilimanus*; 7, *S. acinops* spec. nov.; 8, *S. bicristatus*; 9, *S. gracilis*; 10, *S. dimorphus*

Station	Position	Depth (m)	Date	Species
		Alaminos		
	Gulf of Mexico:			
68-3-3B	25°09'N, 94°11'W	3600	15 Apr 1968	3
68-7-3C	27°36'N, 87°41.5'W	2700	27 Jul 1968	2
68-7-15D	29°10.3'N, 87°31'W	1080	9 Aug 1968	1,2
68-7-13A	29°03'N, 87°15'W	1044	7 Aug 1968	1
68-13-1	25°38'N, 96°07.3'W	864	12 Nov 1968	2
68-13-11	25°23'N, 95°57'W	1350	17 Nov 1968	2
68-13-12A	25°31'N, 95°51'W	1296	17 Nov 1968	1,2
69-11-4	27°24.9'N, 94°44.5'W	990	7 Aug 1969	2
69-11-39	19°01'N, 94°59'W	1368	15 Aug 1969	1
69-11-74	21°29'N, 96°41.5'W	1260	22 Aug 1969	2
69-11-78	21°30'N, 96°55'W	720	23 Aug 1969	1,5
69-11-86	21°41'N, 96°51'W	1062	25 Aug 1969	1,2
69-13-28	25°27'N, 86°04'W	3186	11 Oct 1969	3
69-13-29	25°30'N, 86°09'W	3177	12 Oct 1969	3
69-13-37	26°55'N, 86°48'W	2952	13 Oct 1969	3
69-13-44	28°58'N, 88°28'W	740	15 Oct 1969	1
70-10-58	25°21.3'N, 86°06.5'W	3195	30 Jul 1970	3
71-7-7	26°26.7'N, 96°06'W	864	14 Jul 1971	1
71-7-10	26°32.9'N, 96°06.4'W	922	14 Jul 1971	1,2
71-7-11	26°32.3'N, 96°13.3'W	626	15 Jul 1971	5
71-7-38	27°35.6'N, 92°58.6'W	547	21 Jul 1971	5
71-7-42	27°30.4'N, 92°49.3'W	922	22 Jul 1971	1
71-7-43	27°27.8'N, 92°46'W	1818	22 Jul 1971	1,2
71-7-47	27°32.3'N, 92°47.8'W	864	22 Jul 1971	5
71-7-49	27°26'N, 92°42'W	922	23 Jul 1971	1,2
71-7-56	27°35.8'N, 93°01'W	529	24 Jul 1971	5
71-7-57	26°55.8'N, 92°57.9'W	1215	24 Jul 1971	1
71-8-8	26°08'N, 92°43.9'W	2023	30 Jul 1971	2
71-8-10	26°09'N, 92°48.3'W	2043	30 Jul 1971	2
71-8-13	25°52'N, 93°15.8'W	3213	31 Jul 1971	3
71-8-24	23°56.8'N, 97°05'W	684	3 Aug 1971	5
71-8-29	23°54.7'N, 96°59.9'W	922	4 Aug 1971	1,2
71-8-30	23°49'N, 96°53.9'W	1417	4 Aug 1971	2
71-8-36	23°35.6'N, 96°25.5'W	2117	5 Aug 1971	2
71-8-40	21°16.2'N, 96°51.8'W	558	7 Aug 1971	5
71-8-47	21°35'N, 96°54.6'W	922	7-8 Aug 1971	1,2
71-8-50	21°23.7'N, 96°41.5'W	1197	8-9 Aug 1971	1,2
71-8-57	21°30.3'N, 96°11.7'W	2209	9 Aug 1971	1,2
71-8-60	19°00.3'N, 95°11.1'W	1116	12-13 Aug 1971	1
71-8-67	19°37.5'N, 92°39.2'W	502	13 Aug 1971	5

71-8-75	20°05'N, 92°20'W	1307	15 Aug 1971	1,2,3
72-13-17	23°27.6'N, 97°12.3'W	666	11 Jul 1972	5
72-13-19	23°32.2'N, 97°03.7'W	774	11 Jul 1972	1
72-13-23	23°17.4'N, 97°02.4'W	1062	12 Jul 1972	1,2
72-13-27	23°36.6'N, 96°55.4'W	1417	12 Jul 1972	1,2
72-13-32	26°25'N, 94°47.5'W	1746	13 Jul 1972	2
72-13-39	27°26.4'N, 94°07.6'W	1260	14 Jul 1972	1,2,5
72-13-49	27°40'N, 94°49.8'W	630	16 Jul 1972	1,5
72-13-51	26°55.6'N, 95°10.5'W	1377	17 Jul 1972	1,2
72-13-53	27°24.4'N, 94°56.5'W	1143	17 Jul 1972	1,2
73-2-8	27°21'N, 94°00'W	869	3 Feb 1973	1
		Advance II		
	Northwestern Atlantic:			
78-1-9	38°04.4'N, 70°26.5'W	3850	24 Jun 1978	1,3
78-1-11	37°43.37'N, 70°29.04'W	4086	26 Jun 1978	4
78-1-13	37°46.17'N, 70°27.87'W	3920	27 Jun 1978	4
78-1-14	38°00.02'N, 70°29.73'W	3864	27 Jun 1978	1,3,4
		Albatross		
	Northwestern Atlantic:			
2036	38°52.4'N, 69°24.4'W	3123	18 Jul 1883	1
2037	38°53'N, 69°23.30'W	3116	18 Jul 1883	1,3,4
2038	38°30.30'N, 69°08.25'W	3659	26 Jul 1883	1
2089	39°58.50'N, 70°39.40'W	302	20 Sep 1883	5
2097	37°56.20'N, 70°57.30'W	3451	1 Oct 1883	1,3
2174	38°15'N, 72°03'W	2869	21 Jul 1884	3
2186	39°52.15'N, 70°55.30'W	635	2 Aug 1884	1
2187	39°49.30'N, 71°10'W,	756	3 Aug 1884	1
2212	39°59.30'N, 70°30.55'W	770	22 Aug 1884	1
2226	37°00'N, 71°54'W	3681	10 Sep 1884	4
2429	42°55.5'N, 50°51'W	848	23 Jun 1885	1
2568	39°15'N, 68°08'W	3206	31 Aug 1885	1
2626	32°27.30'N, 77°20.30'W	635	21 Oct 1885	1
2628	32°24'N, 76°55.30'W	950	2 Oct 1885	1
2658	28°21'N, 78°33'W	925	3 May 1886	1
2659	28°32'N, 78°42'W	916	3 May 1886	1
2660	28°40'N, 78°46'W	907	3 May 1886	1
2674	32°32'N, 77°17'W	569	6 May 1886	1
2675	32°32.30'N, 77°15'W	589	6 May 1886	1
2676	32°39'N, 77°01'W	733	6 May 1886	1
2677	32°39'N, 76°50.30'W	860	6 May 1886	1
2678	32°40'N, 76°40.30'W	1316	6 May 1886	2
2713	38°20'N, 70°08.5'W	3346	17 Sep 1886	1,3
	Gulf of Mexico:			
2376	29°03.15'N, 88°16'W	583	11 Feb 1885	5
2383	28°32'N, 88°06'W	2126	3 Mar 1885	2
2385	28°51'N, 88°18'W	1314	3 Mar 1885	1
2392	28°47.5'N, 87°27'W	1303	13 Mar 1885	1,2
2394	28°38.5'N, 87°02'W	756	13 Mar 1885	1

	Bahama Islands:			
2655	27°22'N, 78°07.30'W	608	2 May 1886	6
	Caribbean Sea:			
2125	11°43'N, 69°09.30'W	374	18 Feb 1884	5
	Atlantis			
	North Atlantic:			
152-8	47°10'N, 36°00'W	4140	2 Aug 1948	4
	Eastern Atlantic:			
152-11	42°53.5'N, 29°05'W	1296	10 Aug 1948	1
	Bellows			
	Bahama Islands and Straits of Florida:			
78-1	24°08'N, 80°05'W	362	4 May 1978	9
78-2	24°08'N, 80°05'W	498	14 May 1978	9
78-3	24°09'N, 80°10'W	462	14 May 1978	8,9
78-5	24°00'N, 80°28'W	453	14 May 1978	6,8,9
78-8	23°35'N, 80°22'W	453	15 May 1978	6,9
80-3	24°11'N, 80°03'W	443	19 May 1980	9
Benguela expeditions of the Instituto de Investigaciones Pesqueras de Barcelona, Spain				
	Southeastern Atlantic (Benguela I):			
P-7	–	–	11 Nov 1979	10
	Southeastern Atlantic (Benguela IV):			
P-118	24°08'S, 13°17'E	410	22 Apr 1981	10
P-121	24°53'S, 13°40'E	410	23 Apr 1981	10
P-123	25°05'S, 13°36'E	527	23 Apr 1981	10
P-124	25°08'S, 13°39'E	403	23 Apr 1981	10
P-129	26°10'S, 13°35'E	531	24 Apr 1981	10
P-139	28°10'S, 14°30'E	439	26 Apr 1981	10
	Southeastern Atlantic (Benguela VIII):			
P-29	28°10.8'S, 14°31.2'E	439	13 Jul 1985	10
P-33	29°07.6'S, 14°34.1'E	282	14 Jul 1985	10
P-34	29°17.5'S, 14°31'E	249	14 Jul 1985	10
P-35	29°41.9'S, 14°39'E	425	15 Jul 1985	10
P-36	29°37.8'S, 14°55.2'E	285	15 Jul 1985	10
P-67	23°28.2'S, 13°05.5'E	421	23 Jul 1985	10
	Blake			
	Northwestern Atlantic:			
148	17°17.12'N, 62°46.43'W	374	14 Jan 1879	6
167	16°09.40'N, 61°29.25'W	315	29 Jan 1879	6
309	40°11.40'N, 68°22'W	547	30 Jun 1880	1

	Caribbean Sea and southwestern Atlantic:			
192	15°17.20'N, 61°24.22'W	248	30 Jan 1879	9
210	14°29.10'N, 61°05.47'W	343	12 Feb 1879	9
218	13°49.12'N, 61°04.40'W	295	15 Feb 1879	9
	Straits of Florida:			
5	24°15'N, 82°13'W	412	– – 1877	9
	Calypso			
	Southwestern Atlantic:			
170	37°24.5'S, 54°56'W	132	29 Dec 1961	10
172	37°35'S, 54°53.7'W	270	29 Dec 1961	10
	Challenger			
	Southwestern Atlantic:			
122	09°05'S, 34°50'W	630	10 Sep 1883	9
	Southeastern Atlantic:			
142	35°04'S, 18°37'E	270	18 Dec 1873	9
	Columbus Iselin			
	Northwestern Atlantic:			
73-10-44	36°40.4'N, 74°40'W	335	4 Jun 1973	5
73-10-45	36°41'N, 74°39.8'W	390	4 Jun 1973	5
78-2-2	28°16'N, 77°11'W	1106	19 Feb 1978	1
78-2-14	38°37.2'N, 69°08.6'W	3464	19 Feb 1978	1,3
78-2-23	36°45'N, 71°19.5'W	4243	3 Mar 1978	4
8007-62	29°47'N, 77°09'W	918	21 Sep 1980	1
8007-63	28°06'N, 77°08'W	1093	21 Sep 1980	1
8007-64	28°56'N, 77°17'W	1086	21 Sep 1980	1,2
8007-70	27°50'N, 77°22'W	1171	24 Sep 1980	1,2
	Bahama Islands and Straits of Florida:			
5	25°10'N, 77°10'W	549	2 Jul 1972	9
8	24°01'N, 77°23.4'W	1380	3 Jul 1972	7
9	23°51.8'N, 77°05.7'W	1318	4 Jul 1972	2,7
10	23°47'N, 76°47'W	1300	4 Jul 1972	2
12	23°32'N, 76°55'W	1290	4 Jul 1972	2,7
13	23°25.5'N, 77°08'W	500	4 Jul 1972	2
14	23°35.2'N, 77°11.2'W	1246	5 Jul 1972	2,7
19	24°02.1'N, 77°17.1'W	1335	5 Jul 1972	7
21	24°26.9'N, 77°24.75'W	1545	6 Jul 1972	2
30	25°17'N, 77°50.2'W	2542	7 Jul 1972	3
7203-32	25°17'N, 77°33'W	3017	8 Jul 1972	1
7203-33	25°26.2'N, 77°20.5'W	1780	8-9 Jul 1972	1
40	23°46.75'N, 76°58.9'W	1307	22 Feb 1973	2
42	23°31'N, 76°44'W	1280	23 Feb 1973	2,7
43	23°31'N, 76°58'W	1317	23 Feb 1973	2,7
44	23°36'N, 77°14'W	1280	23 Feb 1973	7
47	23°40'N, 77°07.9'W	1322	24 Feb 1973	2

52	23°37'N, 77°00'W	850	25 Feb 1973	2
54	23°53.4'N, 77°10.1'W	1298	26 Feb 1973	2,7
57	24°03.3'N, 77°23.1'W	1400	27 Feb 1973	2,7
58	24°14.2'N, 77°17.9'W	1390	27 Feb 1973	2,7
60	24°23'N, 77°25.2'W	1527	28 Feb 1973	7
61	24°26.5'N, 77°20'W	1463	28 Feb 1973	2,7
66	24°43.75'N, 76°35.7'W	1545	2 Mar 1973	2
71	24°21'N, 75°59.5'W	1682	7 Mar 1973	2
78	24°24.7'N, 76°11.3'W	1683	6 Mar 1973	2
79	23°50.5'N, 76°49'W	1271	8 Mar 1973	2,7
80	23°52.7'N, 77°01.8'W	1280	8 Mar 1973	2
106	23°51.2'N, 76°54.9'W	1311	21 Sep 1973	2,7
110	23°40'N, 77°01.7'W	1360	22 Sep 1973	2,7
111	23°36.2'N, 77°13.3'W	1342	22 Sep 1973	7
113	23°41.2'N, 77°06.5'W	1368	23 Sep 1973	7
116	23°29.5'N, 76°56.4'W	1297	23 Sep 1973	2
123	24°11.1'N, 77°17'W	1385	24 Sep 1973	2
140	26°24.1'N, 79°35.7'W	738	28 Sep 1974	1
154	23°32.2'N, 76°46.1'W	1311	4 Feb 1974	2,7
156	23°43'N, 76°50'W	1334	5 Feb 1974	2,7
161	23°40'N, 77°06.2'W	1370	6 Feb 1974	2,7
163	23°32.5'N, 77°09.9'W	1342	6 Feb 1974	2,7
164	23°44.7'N, 77°13'W	1372	6 Feb 1974	2,7
165	24°02.8'N, 77°22.1'W	1426	6-7 Feb 1974	2
167	23°38'N, 77°17.2'W	1523	7 Feb 1974	2,7
176	24°39'N, 76°29.2'W	1632	10 Feb 1974	2
178	24°15.5'N, 76°06.5'W	1790	10 Feb 1974	2
183	23°45'N, 75°38.9'W	1814	11 Feb 1974	2
186	23°45.2'N, 75°41.6'W	1853	12 Feb 1974	2
187	23°59'N, 75°49'W	1880	12 Feb 1974	2
191	24°09.5'N, 75°56'W	1840	13 Feb 1974	2
192	24°20.9'N, 75°59.4'W	1760	13 Feb 1974	2
247	24°38.6'N, 77°32.5'W	1732	30 Oct 1974	2
249	23°47.7'N, 77°03'W	1372	31 Oct 1974	7
250	23°52'N, 76°52.3'W	1311	31 Oct 1974	2
252	23°38.7'N, 76°45.2'W	1332	1 Nov 1974	2,7
264	23°53.4'N, 77°08.9'W	1335	3 Nov 1974	7
271	24°17'N, 77°26'W	1502	4 Nov 1974	7
272	24°04.6'N, 77°22.8'W	1445	4 Nov 1974	2
274	24°31.75'N, 76°17'W	1701	6-7 Nov 1974	2
275	24°38.9'N, 76°26'W	1630	7 Nov 1974	2
277	24°14.2'N, 76°06'W	1794	7 Nov 1974	2
278	23°56.2'N, 75°58.4'W	1779	8 Nov 1974	2
279	23°49.75'N, 75°49.8'W	1853	8 Nov 1974	2
280	23°51.75'N, 75°16.3'W	2347	8 Nov 1974	2
282	23°59.7'N, 75°46.75'W	1908	9 Nov 1974	2
284	23°56.8'N, 75°59.2'W	1781	9 Nov 1974	2
285	24°15.25'N, 75°54.9'W	1767	9 Nov 1974	2
286	24°09.7'N, 75°54.8'W	1842	10 Nov 1974	2
287	24°21.7'N, 76°01'W	1741	10 Nov 1974	2
288	25°16'N, 77°42.6'W	2830	11 Nov 1974	2
289	26°10.4'N, 78°58.7'W	351	11 Nov 1974	6
299	24°39.2'N, 77°33'W	957	2 Apr 1975	2
303	23°56.1'N, 77°19'W	1390	4 Apr 1975	7

304	23°48.5'N, 77°05.2'W	1366	4 Apr 1975	2,7
306	24°06.2'N, 77°17.9'W	1379	4-5 Apr 1975	7
311	23°37.6'N, 77°14.1'W	1353	6 Apr 1975	2,7
312	23°35.7'N, 77°10.7'W	1348	6 Apr 1975	2,7
315	24°30.2'N, 77°22.3'W	1517	7 Apr 1975	2,7
319	23°33.3'N, 76°44.8'W	1295	8 Apr 1975	2,7
324	23°31.3'N, 76°56.5'W	1333	9 Apr 1975	2
326	23°51.2'N, 77°11'W	1383	9-10 Apr 1975	2,7
333	24°23.5'N, 76°07.5'W	1767	12 Apr 1975	3
334	24°15.3'N, 76°06.3'W	1789	13 Apr 1975	2
340	24°19.75'N, 75°59.75'W	1746	15 Apr 1975	2
344	23°55'N, 75°27.2'W	2178	16 Apr 1975	2
345	23°48.9'N, 75°14.2'W	2360	16 Apr 1975	2
350	24°02.5'N, 77°23.5'W	1426	4 Apr 1975	7
353	25°15.7'N, 77°39.3'W	2977	21 Apr 1975	1,3
356	24°23.2'N, 77°25.5'W	1561	20 Aug 1975	2,7
363	23°51.4'N, 76°54.8'W	1324	22 Aug 1975	2,7
367	23°51.25'N, 76°53.6'W	1324	22-23 Aug 1975	2
368	23°42.2'N, 76°52'W	1352	23 Aug 1975	2
375	25°16.3'N, 77°37.25'W	3050	24 Aug 1975	1
376	23°55.3'N, 75°58.6'W	1767	26 Aug 1975	2
377	23°59.8'N, 75°46'W	1917	27 Aug 1975	2
378	24°21.3'N, 76°03.5'W	1746	26-27 Aug 1975	2
379	24°32.75'N, 76°17.2'W	1645	27 Aug 1975	3
380	24°38.6'N, 76°25.6'W	1635	27 Aug 1975	2
381	24°23.2'N, 76°09.4'W	1758	27 Aug 1975	2
382	23°56.8'N, 76°00.75'W	1763	28 Aug 1975	2
383	23°49.5'N, 75°49.25'W	1844	28 Aug 1975	2
384	24°09'N, 75°54.8'W	1844	28 Aug 1975	2
385	24°13.8'N, 76°06.1'W	1792	28-29 Aug 1975	2
388	23°56'N, 75°31.7'W	2133	29 Aug 1975	2
392	22°48'N, 75°38'W	2259	31 Aug 1975	2
393	22°15.16'N, 75°05.75'W	2624	31 Aug 1975	2
395	22°00.8'N, 75°04.25'W	2681	1 Sep 1975	1
403	23°56.8'N, 75°26.8'W	2171	5 Sep 1975	2
406	23°59.1'N, 77°22.7'W	1408	28 Feb 1976	2,7
410	23°30.3'N, 76°51'W	1323	29 Feb 1976	2
420	24°00.5'N, 77°10.75'W	474	2 Mar 1976	9
425	25°16.2'N, 77°51.8'W	2537	3-4 Mar 1976	7
434	23°40.8'N, 77°16.8'W	1337	8 Mar 1976	2
C001	25°23'N, 77°02'W	2451	29 Aug 1980	1
8007-8	24°14'N, 76°06'W	1787	2 Sep 1980	2
D004	21°57'N, 74°46'W	2728	16 Nov 1981	1
D005	22°03'N, 74°48'W	2728	16 Nov 1981	1,3
D007	21°50'N, 74°56'W	2758	17 Nov 1981	1,3
D010	21°24'N, 74°05'W	2703	18 Nov 1981	1

Combat

Bahama Islands and Straits of Florida:

237	27°28'N, 78°44'W	387	3 Feb 1957	6
447	25°07'N, 79°15'W	540	23 Jul 1957	6
452	24 35'N, 79 58'W	1017	25 Jul 1957	1

		Eastward		
	Northwestern Atlantic:			
7558	33°15.5'N, 75°30'W	3420	17 Jun 1967	1,3
67-41-8226	33°51'N, 75°25.5'W	–	6 Oct 1967	1,3
67-41-8228	34°02'N, 75°30'W	2930	6 Oct 1967	1
67-41	34°03.5'N, 75°32'W	2930	6 Oct 1967	3
73-1-59	34°03.2'N, 75°52'W	550	29 Apr 1973	1
74-2-6	35°23.2'N, 74°43.4'W	2105	16 Apr 1974	3
74-2-28	37°07.6'N, 74°19.4'W	1607	18 Apr 1974	1
75-6-22	36°48'N, 73°32.7'W	2937	25 Jul 1975	1,3
75-6-29	38°51'N, 72°44.1'W	1275	28 Jul 1975	1
	Straits of Florida:			
26538	27°12.6'N, 79°13.7'W	420	29 Mar 1975	6
		Eltanin		
	Southwestern Atlantic:			
740	56°06.07'S, 66°19.30'W	549	18 Sep 1963	10
	Southeastern Pacific:			
326	46°04'S, 83°55'W	298	9 Oct 1966	10
1283	43°13'S, 97°43'W	146	13 Sep 1964	10
1346	54°49'S, 129°48'W	549	7 Nov 1964	10
		Fish Hawk		
	Straits of Florida:			
7286	24°18'N, 81°47.45'W	239	19 Feb 1902	9
		Gerda		
	Northwestern Atlantic:			
181	27°55'N, 78°59'W	779	2 Jul 1963	1
182	27°57'N, 78°40'W	897	2 Jul 1963	1
403	27°48'N, 78°40'W	–	20 Sep 1964	1
670	28°10'N, 79°00'W	805	18 Jul 1965	1
	Bahama Islands and Straits of Florida:			
17	25°45'N, 80°00'W	252	30 May 1962	1
136	24°21'N, 80°36'W	751	21-22 Jun 1963	1
158	26°27'N, 79°21'W	540	25 Jun 1963	9
220	24°33'N, 80°31'W	320	22 Jan 1964	9
223	24°21'N, 80°23'W	915	23 Jan 1964	1
233	25°41'N, 79°23'W	439	30 Jan 1964	9
234	25°44'N, 79°22'W	474	30 Jan 1964	6
235	25°46.5'N, 79°22'W	531	30 Jan 1964	9
288	24°13'N, 81°36'W	595	3 Apr 1964	8
299	26°16'N, 79°30'W	641	5 Apr 1964	8
301	26°38'N, 79°21'W	648	5 Apr 1964	8
366	24°13'N, 81°08'W	709	15 Sep 1964	1
370	23°53'N, 81°16'W	1281	16 Sep 1964	2

374	23°50'N, 81°37'W	1241	17 Sep 1964	2
432	24°18'N, 82°33'W	–	28 Nov 1964	9
437	24°16'N, 82°14'W	384	28 Nov 1964	9
448	23°53'N, 82°17'W	1148	1 Dec 1964	1
465	24°17'N, 82°51'W	403	25 Jan 1965	9
482	24°32'N, 80°48'W	210	26 Jan 1965	6
507	25°53'N, 79°19'W	384	2 Mar 1965	6
524	26°21'N, 78°44'W	715	3 Mar 1965	6
525	26°28'N, 78°40'W	403	3 Mar 1965	6
526	26°28'N, 78°40'W	403	3 Mar 1965	6
580	24°27'N, 81°27'W	146	14 Apr 1965	9
637	26°05'N, 79°13'W	201	30 Jun 1965	6
658	27°18'N, 79°44'W	320	16 Jul 1965	6
698	10°45.5'N, 62°02.5'W	85	22 Jul 1965	6
711	26°23'N, 78°45'W	851	23 Jul 1965	1
715	26°05'N, 79°24'W	549	2 Aug 1965	9
721	26°22'N 79°02'W	494	3 Aug 1965	9
722	26°13'N, 78°54'W	393	3 Aug 1965	6
798	26°00'N, 79°17.5'W	403	12 Sep 1966	6
801	26°17'N, 79°20'W	452	12 Sep 1966	9
806	26°23'N, 79°23'W	549	13 Sep 1966	9
815	24°08'N, 79°48'W	618	22 Jun 1967	8
819	23°40'N, 79°05'W	494	22 Jun 1967	6
835	24°22'N, 81°11'W	198	11 Jul 1967	6
846	25°46'N, 80°03'W	194	2 Aug 1967	9
864	24°31'N, 80°58'W	171	29 Aug 1967	6
867	24°05'N, 80°50'W	792	30 Aug 1967	1
870	24°17'N, 80°42'W	794	30 Aug 1967	1
876	24°05'N, 79°49'W	261	31 Aug 1967	6
909	26°12'N, 79°19'W	441	25 Sep 1967	6
929	26°13'N, 78°57'W	414	29 Sep 1967	6
935	27°37'N, 78°52'W	459	30 Sep 1967	6
954	21°11'N, 86°30'W	306	28 Jan 1968	6
960	23°30'N, 82°26'W	1670	31 Jan 1968	1,2
961	23°47'N, 82°00'W	1656	31 Jan 1968	2
963	23°41'N, 82°16'W	1431	1 Feb 1968	2
967	24°15'N, 82°26'W	495	2 Feb 1968	9
968	24°17'N, 82°34'W	430	2 Feb 1968	9
972	24°24'N, 80°52'W	227	3 Feb 1968	9
1083	24°18.5'N, 82°20'W	167	26 Apr 1969	6
1102	24°15.5'N, 81°34'W	284	29 Apr 1969	9
1312	26°38.4'N, 79°02.5'W	527	31 Mar 1971	6
	Caribbean Sea:			
878	21°10'N, 86°24'W	–	7-8 Sep 1967	9
893	21°10'N, 86°21'W	320	10 Sep 1967	6
894	21°11'N, 86°19'W	203	10 Sep 1967	6
897	20°59'N, 86°24'W	288	10 Sep 1967	6
951	21°06'N, 86°28'W	302	28 Jan 1968	6
		Gloucester Fisheries		
212	Off Massachusetts	–	–	1

James M. Gilliss

	Northwestern Atlantic:			
74-4-2	36°00.5'N, 74°45.5'W	410	11 Oct 1974	1
74-4-85	36°37'N, 73°21.8'W	1823	19 Nov 1974	1
74-4-105	37°05.4'N, 74°23.6'W	1520	24 Nov 1974	1
75-8-4	33°33.4'N, 76°03.8'W	980	7 Sep 1975	1
75-8-27	37°09.9'N, 74°24.8'W	1287	12 Dec 1975	1
75-8-36	36°59'N, 72°58'W	3083	15 Sep 1975	1,3
75-8-79	36°44.6'N, 74°41'W	102	1 Sep 1975	1
76-1-28	37°01.3'N, 74°13.6'W	1916	24 Jan 1976	1
76-1-54	36°49'N, 74°25'W	2000	28 Jan 1976	1
	Straits of Florida:			
134	24°12.11'N, 80°52.3'W	867	27 Jul 1975	1
	Caribbean Sea:			
37	12°00'N, 75°07'W	3365	2 Aug 1972	3
	Eastern Atlantic:			
93	06°30'N, 22°06'W	3446	19 Aug 1973	1,3

John Elliott Pillsbury

	Northwestern Atlantic:			
120	31°49'N, 76°26'W	2340	29 Jul 1964	1,3
	Bahama Islands and Straits of Florida:			
586	23°28.5'N, 82°36'W	1737	24 May 1967	1
1429	21°19.2'N, 73°45.5'W	2532	21 Jul 1971	1
	Caribbean Sea and southwestern Atlantic:			
325	09°52'N, 79°35.5'W	1774	7 Jul 1966	2
328	09°55'N, 79°04'W	2050	8 Jul 1966	2
340	09°13'N, 77°46'W	362	9 Jul 1966	6,9
346	09°51'N, 76°58'W	2950	10 Jul 1966	3
374	09°52'N, 76°10.6'W	434	14 Jul 1966	9
377	09°50.5'N, 78°39.3'W	1836	8-9 Jul 1966	2
391	10°03'N, 76°27'W	1215	16 Jul 1966	1,2
394	09°28'N, 76°27'W	531	16 Jul 1966	9
407	09°00.2'N, 77°25.3'W	1152	18 Jul 1966	1,2
445	09°00.3'N, 81°25'W	342	21 Jul 1966	6
447	09°04'N, 81°13.8'W	673	21 Jul 1966	1
448	09°10.1'N, 80°55.6'W	947	21 Jul 1966	2
478	11°32'N, 62°07.2'W	598	2 Aug 1966	5
589	21°14'N, 86°26'W	484	14 Mar 1967	8,9
598	21°07'N, 86°21'W	202	15 Mar 1968	6
605	18°50.1'N, 87°31.5'W	707	17 Mar 1968	1,8
606	18°45'N, 87°33'W	639	17 Mar 1968	8
607	18°30'N, 87°37'W	774	17 Mar 1968	1
610	17°03'N, 87°38.5'W	324	18 Mar 1968	9
673	07°56'N, 54°39'W	1026	11 Jul 1968	1

681	08°11.5'N, 56°12'W	2691	14 Jul 1968	3
776	12°13.3'N, 72°50'W	400	29 Jul 1968	9
847	11°37.3'N, 60°59.4'W	905	2 Jul 1969	1
876	13°13.9'N, 61°04.7'W	257	6 Jul 1969	9
1178	19°14'N, 73°14'W	1769	30 Jun 1970	2
1181	18°51'N, 74°30'W	2506	1 Jul 1970	2
1224	17°31.2'N, 77°49.2'W	893	6 Jul 1970	1
1354	14°21'N, 81°55'W	263	31 Jan 1971	6
1444	22°31.5'N, 75°23.6'W	2450	24 Jul 1971	2
	Eastern Atlantic:			
51	04°56'N, 05°01'W	369	31 May 1964	9
53	04°50'N, 04°55'W	1553	31 May 1964	2
74	04°20'N, 09°26'W	720	4 Jun 1964	1,3
	LGL Ecological Research Associates			
	Gulf of Mexico:			
C2-194	27°53.3'N, 90°05.3'W	786	27 Nov 1983	1
C3-225	27°48'N, 90°03'W	850	27 Nov 1983	2,8
W1-2022	27°37'N, 93°33.6'W	342	4 Apr 1984	5
W4-2103	26°44.4'N, 93°18.6'W	1454	Apr 1984	2
W5-2125	26°17.1'N, 93°21.8'W	2322	10 Apr 1984	5
C2-2256	27°54.4'N, 90°06'W	603	12 Apr 1984	1,5
E4-2429	28°06'N, 86°35.3'W	1170	18 Apr 1984	1
	Johnson Smithsonian Deep-Sea Expedition			
	Caribbean Sea:			
100	18°40.15'N, 64°50.15'W	270	4 Mar 1933	6
	Michael Sars			
	Eastern Atlantic:			
–	34°59'N, 33°01'W	–	9 Jun 1910	1
	Oregon and Oregon II			
	Northwestern Atlantic:			
10660	36°31'N, 74°43'W	468	23 Jul 1969	1
	Gulf of Mexico:			
127	29°02'N, 88°34'W	464	23 Sep 1950	5
163	27°15'N, 96°00'W	823	28 Nov 1950	5
307	29°00'N, 88°35'W	396	22 Apr 1951	5
319	29°20'N, 87°25'W	567	28 Apr 1951	1,5
382	29°11.5'N, 88°07.5'W	360	21 Jun 1951	5
482	28°57'N, 88°42.5'W	378	7 Sep 1951	5
516	29°16.4'N, 87°39.5'W	472	1 Apr 1952	5
1303	28°47'N, 87°50'W	2160	26 May 1955	2
1424	29°06'N, 88°02'W	720	23 Sep 1955	1
1507	27°43'N, 95°05'W	540	6 May 1956	5
1564	29°10'N, 88°08'W	432	22 Jun 1956	5
2202	28°58'N, 88°11'W	1125	26 Jun 1958	1

2574	26°34'N, 89°53'W	2610	28 Jul 1959	2,3
3650	29°12.5'N, 88°01'W	360	25 Jul 1962	5
3652	29°12.5'N, 87°56.5'W	450	25 Jul 1962	5
3654	29°08.5'N, 88°00.5'W	738	25 Jul 1962	1
3657	29°06.5'N, 87°57'W	990	26 Jul 1962	1
3658	28°56.5'N, 88°19.5'W	1350	27 Jul 1962	1
3660	29°10'N, 87°57'W	720	27 Jul 1962	1
3662	29°10.5'N, 88°01'W	1008	28 Jul 1962	1
3663	28°56'N, 88°08'W	1575	28 Jul 1962	1,2
3664	28°49'N, 88°03'W	1800	28 Jul 1972	1
3666	28°48.5'N, 88°24.5'W	1170	29 Jul 1972	1,2
3679	29°14.5'N, 87°49.5'W	405	7 Aug 1962	5
4566	23°05'N, 86°09'W	1260	6 Dec 1963	2
4567	23°08'N, 86°22'W	1080	7 Dec 1963	2
4571	23°04'N, 86°37'W	720	7 Dec 1963	1
4701	27°42'N, 90°32.5'W	900	22 Feb 1964	1
4703	27°55'N, 90°28'W	540	22 Feb 1964	5
4709	27°45'N, 91°18.5'W	540	23 Feb 1964	5
4713	27°34'N, 92°10'W	900	24 Feb 1964	1
10329	29°06'N, 88°22'W	403	15 Jan 1969	5
10388	29°08'N, 88°15'W	432	25 Feb 1969	5
10636	28°17'N, 86°21'W	661	20 Jun 1969	1
10641	29°16'N, 87°42'W	414	22 Jun 1969	5
10874	28°33'N, 87°09'W	1098	15 Jan 1970	1
10875	28°42'N, 87°18'W	1188	15 Jan 1970	1
10876	28°55'N, 87°23'W	1440	15 Jan 1970	1
10877	28°34'N, 87°26'W	1620	16 Jan 1970	1
10878	28°54'N, 87°29'W	1800	16 Jan 1970	1
10879	25°23'N, 96°14'W	963	19 Jan 1970	1
10895	28°49'N, 88°27'W	1269	27 Jan 1970	1
11193	29°19'N, 86°47'W	486	29 Aug 1970	5
11204	29°12'N, 87°55'W	540	1 Sep 1970	5
11552	28°24'N, 89°19'W	594	27 Sep 1971	1,5
	Caribbean Sea and southwestern Atlantic:			
1890	16°35'N, 80°55'W	180	24 Aug 1957	5
1900	10°40'N, 82°50'W	2034	8 Sep 1957	6
2011	07°46'N, 54°36'W	720	7 Nov 1957	5
2030	07°10'N, 52°55'W	540	10 Nov 1957	1
2627	18°05'N, 65°21'W	216	29 Sep 1959	6
2648	18°13'N, 67°21'W	360	6 Oct 1959	6
2771	11°40'N, 62°27'W	396	15 Apr 1960	5,9
3549	17°50'N, 77°52'W	306	16 Oct 1962	6
3583	09°16'N, 81°37'W	504	25 May 1962	5
3584	09°13'N, 81°30'W	360	25 May 1962	9
3601	09°07'N, 81°10'W	720	31 May 1962	1
3627	16°50'N, 81°21'W	360	17 Jun 1962	6
3637	17°13'N, 87°55'W	306	10 Jun 1962	6
4226	00°18'N, 44°17'W	270	9 Mar 1963	8,9
4293	07°14'N, 52°55'W	720	21 Mar 1963	1,5
4294	07°21'N, 53°15'W	540	21 Mar 1963	1,5
4296	07°55'N, 53°55'W	900	22 Mar 1963	1
4299	07°46'N, 54°00'W	720	23 Mar 1963	1
4398	12°46'N, 70°41'W	198	26 Sep 1963	9

4407	11°59'N, 69°30'W	414	27 Sep 1963	5
4412	11°49'N, 69°24'W	540	3 Oct 1963	1
4415	12°02'N, 69°21'W	810	3 Oct 1963	1
4423	11°53'N, 69°28'W	342	5 Oct 1963	9
4428	11°41'N, 68°57'W	720	6 Oct 1963	1
4842	11°10'N, 74°27'W	504	17 May 1964	5
4911	11°50'N, 73°05'W	342	31 May 1964	6
4941	20°59'N, 86°29'W	198	12 Jun 1964	6
5028	11°30'N, 60°46'W	432	22 Sep 1964	5
5624	10°52'N, 66°08'W	101	25 Sep 1965	6
5638	11°30'N, 68°35'W	450	30 Sep 1965	5
5929	15°39'N, 61°10'W	639	5 Mar 1966	1
5930	15°38'N, 61°07'W	796	5 Mar 1966	1
5956	13°40'N, 60°54'W	225	10 Mar 1966	6
6697	17°47'N, 63°09'W	828	18 May 1967	1
6699	17°38.5'N, 62°16'W	333	19 May 1967	6
6703	16°53'N, 61°53'W	828	21 May 1967	1
6706	17°25'N, 62°56'W	270	22 May 1967	6
6715	18°36'N, 63°27'W	234	30 May 1967	6
10491	10°28'N, 60°04'W	639	25 Apr 1969	1
10492	10°19'N, 59°57'W	657	25 Apr 1969	1
10602	07°46'N, 54°35'W	538	10 May 1969	5
10604	07°49'N, 54°22'W	720	10 May 1969	1
10607	07°42'N, 53°36'W	770	11 May 1969	1
10610	07°20'N, 53°02'W	720	12 May 1969	1
10611	07°13'N, 52°52'W	756	12 May 1969	1
10614	07°06'N, 52°44'W	657	13 May 1969	5
10615	07°22'N, 53°02'W	711	13 May 1969	1
10618	07°51'N, 54°42'W	810	15 May 1969	1
10799	07°31'N, 53°11'W	716	17 Nov 1969	1
10823	07°40'N, 53°53'W	540	27 Nov 1969	5
10834	18°18'N, 63°23'W	677	6 Dec 1969	1
10847	18°18'N, 63°24'W	648	10 Dec 1969	1
11276	11°17'N, 74°40'W	810	14 Nov 1970	5
		Panulirus II		
	Bermuda:			
–	32°19'N, 64°36'W	730	24 Sep 1974	6
		Pieter Faure		
	Off South Africa:			
1879	Cape St. Blaize, N. by E. 73 miles	225	–	10
		Silver Bay		
	Northwestern Atlantic:			
446	28°05'N, 78°24'W	1062	10 Jun 1958	1
	Gulf of Mexico:			
1196	24°11'N, 83°21.5'W	720	8 Jun 1959	1

	Bahama Islands and Straits of Florida:			
2416	24°18'N, 81°29'W	225	28 Oct 1960	6,9
2443	24°08'N, 80°09'W	360	2 Nov 1960	6
2481	26°08'N, 79°11.5'W	360	9 Nov 1960	6
3513	23°26'N, 79°24'W	585	8 Nov 1961	9
	Snellius expedition 1966			
	Southwestern Atlantic:			
F36	07°26.8'N, 56°21.8'W	410	5 May 1966	5
	Talisman			
	Eastern Atlantic:			
86	22°55'N, 17°29'W	930	12 Jul 1883	1
111	Cape Verde Islands	580	–	8
134	42°19'N, 23°36'W	4100	24 Aug 1883	4
	Tydeman (Rockall cruise; and Cancap: II-VI expeditions of the Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands; cf. van der Land, 1987)			
	West of Ireland (Rockall cruise):			
6	53°24'N, 16°25'W	2880	10 Jun 1977	1
	Canary Islands (Cancap II):			
2.006	27°47'N, 14°24'W	2050	23 Aug 1977	2
2.020	27°40'N, 14°20'W	–	25 Aug 1977	2
2.026	27°50'N, 14°29'W	2200	25 Aug 1977	2
2.027	27°56'N, 14°28'W	1540	25 Aug 1977	2
2.067	27°58'N, 14°12'W	1830	29 Aug 1977	2
2.087	27°42'N, 15°02'W	2300	31 Aug 1977	2
2.090	27°15'N, 18°03'W	3730	2 Sep 1977	1
2.112	27°13'N, 18°07'W	3750	4 Sep 1977	3
2.133	27°40'N, 18°10'W	1000	8 Sep 1977	8
2.135	27°41'N, 18°11'W	1370	8 Sep 1977	8
2.148	27°40'N, 18°03'W	700	9 Sep 1977	8
	Madeira and Mauritania (Cancap III):			
3.020	32°53'N, 16°21'W	3120	15 Oct 1978	3
3.052	32°25'N, 16°54'W	3065	19 Oct 1978	1,3
3.053	32°25'N, 16°57'W	3010	20 Oct 1978	1,3
3.077	29°54'N, 15°53'W	–	21 Oct 1978	1,3
3.078	29°53'N, 15°53'W	–	22 Oct 1978	1,3
3.094	29°54'N, 15°52'W	–	22 Oct 1978	1,3
3.105	29°50'N, 15°46'W	3550	24 Oct 1978	1,3
	Selvagens and Canary Islands (Cancap IV):			
4.053	28°43'N, 13°23'W	1352	17-18 May 1980	3
4.054	28°45'N, 13°19'W	1315	18 May 1980	2
4.056	28°47'N, 13°22'W	1345	8 May 1980	3
4.057	28°47'N, 13°24'W	1335	19 May 1980	2

4.066	28°50'N, 13°37'W	1070	20 May 1980	1,8
4.107	30°03'N, 15°52'W	2500	26-27 May 1980	3
4.126	28°28'N, 18°18'W	3590	29-30 May 1980	1
4.132	28°30'N, 18°16'W	3360	30 May 1980	1,2
4.154	28°37'N, 18°15'W	3300	3 Jun 1980	3
4.166	29°48'N, 15°56'W	3570	6 Jun 1980	1,3
4.180	32°48'N, 16°18'W	3499	9-10 Jun 1980	1,3
	Azores (Cancap V):			
5.001	38°10'N, 24°52'W	3150	23 May 1981	1,3
5.003	38°03'N, 24°45'W	2850	24 May 1981	1,3
5.004	38°06'N, 24°49'W	3100	24 May 1981	1,3
5.005	37°55'N, 24°46'W	2050	24 May 1981	3
5.024	37°17'N, 25°14'W	2120	28 May 1981	2
5.042	36°50'N, 24°42'W	2950	28 May 1981	1,3
5.043	36°46'N, 24°44'W	2950	29 May 1981	1,3
5.048	36°50'N, 25°28'W	2480	29 May 1981	3
5.049	36°49'N, 25°25'W	2450	30 May 1981	1,3
5.090	38°09'N, 28°31'W	1350	2 Jun 1981	1,3
5.183	39°21'N, 30°52'W	1890	12 Jun 1981	3
	Cape Verde Islands (Cancap VI):			
6.046	14°41'N, 24°30'W	3550	10 Jun 1982	3
6.053	14°40'N, 24°06'W	3850	10-11 Jun 1982	4
6.055	15°46'N, 22°38'W	2220	11 Jun 1982	2,3
6.092	16°23'N, 24°37'W	3250	14-15 Jun 1982	1,3
6.122	17°00'N, 25°21'W	646	18 Jun 1982	8
	U. S. Fish Commission			
	Northwestern Atlantic:			
212	42°40'N, 63°06'W	–	–	1
880	–	454	13 Sep 1880	1
894	39°53'N, 70°58.30'W	657	2 Oct 1880	1
895	39°56.30'N, 70°59.45'W	428	2 Oct 1880	5
898	Off mouth of Chesapeake Bay	540	1880	1
924	39°57.30'N, 70°46'W	288	16 Jul 1881	5
939	39°53'N, 69°50.30'W	464	4 Aug 1880	5
947	39°56.30'N, 71°13.30'W	562	9 Aug 1881	1
994	39°40'N, 71°30'W	662	8 Sep 1881	1
1029	–	–	14 Sep 1881	1
1124	40°01'N, 68°54'W	1152	26 Aug 1882	1
	Miscellaneous stations			
	Western Atlantic:			
	Western Dry Rocks, Florida	259	1916	9
	Tortugas, Florida; coll.: Darby	–	1934	1
	25 mi south of Loggerhead Key, Tortugas, Florida; coll.: Darby	540	Jul 1936	1
	coll.: Schmitt	–	1939	1

Tortugas, Florida; coll.: Schmitt	509	–	1
North American Basin, off North Carolina	2500	–	2
Bahama Islands; coll.: Sulak and Carney	–	–	2
Barbados; coll.: Lewis	–	–	9
Eastern Atlantic:			
45°10'N, 02°20'W	–	21 Dec 1972	1
Southeastern Atlantic:			
25°52'S, 13°52'E	340	–	10
29°09'S, 14°31'E	310	–	10
WNW of Cape Columbine	396	1959	10

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