

## VERIANDER

The systematics of the genus *Arthroporus* Haldeman, 1847, and a new genus for *Arthroporus* from Forest, 1966. (Crustacea: Decapoda: Paguridae)

J. G. REYNOLDS

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TO MY FRIEND AND COLLEAGUE JIM,  
WITH MY WARMEST WISHES,

Julio  
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The systematics of the genus *Anapagurus*  
Henderson, 1886, and a new genus for  
*Anapagurus drachi* Forest, 1966  
(Crustacea: Decapoda: Paguridae)

J. García-Gómez



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/ J. García-Gómez

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# The systematics of the genus *Anapagurus* Henderson, 1886, and a new genus for *Anapagurus drachi* Forest, 1966 (Crustacea: Decapoda: Paguridae)

J. García-Gómez

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Key words: Hermit crabs; *Anapagurus*; systematic revision; new species; symbiotic associations; *Forestopagurus* new genus.

A worldwide systematic review of the genus *Anapagurus* is presented. In addition to the rediagnoses of the genus and all known species, five new species, *A. alboranensis*, *A. adriaticus*, *A. vossi*, *A. atlantidii*, and *A. congolensis*, are described. All 18 species are illustrated and a key to the species is given. Several new diagnostic characters found in the right chelipeds (1- the shape and relative size of the mesial and lateral lobes that flank the dorsoproximal margin of the palm; 2- the shape and relative size of the median sinus of the ventroproximal palmar margin; 3- the shape, armature and relative size of the dorsomesial distal carpal angle; and 4- the shape and extension of both ventrodiscal and ventroproximal carpal margins, which determine the relative ventral length); the relative length and setation of the ultimate antennular segment; and the relative length between the right uropodal endopod and the distal protopodal lobe have been used. A number of systematic problems are clarified. *Anapagurus pusillus* Henderson, 1888 is reinstated. *Anapagurus brevicarpus* A. Milne Edwards & Bouvier, 1892 is found to be a junior synonym of *A. chiroacanthus* (Lilljeborg, 1856). *Anapagurus acutus* and *A. marginatus* described by A. Milne Edwards & Bouvier, 1893, are excluded from *Anapagurus* and considered species incertae sedis. *Anapagurus drachi* Forest, 1966, is removed from *Anapagurus*, and placed in a new genus, *Forestopagurus*.

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## Introduction

The genus *Anapagurus* was described by Henderson (1886a) as a subgenus of *Spiropagurus* Stimpson, 1858, based on differences in the sexual tubes, chelipeds and walking pereopods of three species collected in the Firth of Clyde, Scotland that he removed from *Pagurus*, *P. hyndmanni*, *P. laevis*, and *P. ferrugineus*. The same year, Norman (1886) considered the latter species a junior synonym of *P. chiroacanthus*. Two years later, Henderson (1888) elevated *Anapagurus* to the generic rank and added two new species, *A. pusillus* from off the Azores and Canary Islands, and *A. australiensis* [= *Micropagurus acantholepis* (Stimpson, 1858); see Gunn & McLaughlin, 1988] from Port Jackson, Australia.

In 1892 four new species were added to *Anapagurus*, *A. curvidactylus* from off Dakar, Senegal by Chevreux & Bouvier; *A. brevicarpus* from off northern Spain and Arguin Bank, Mauritania, and *A. bicorniger* from Golfo de Cádiz, Spain by A. Milne Edwards & Bouvier; and *A. pusillus* var. *japonica* (= *A. japonicus*) from Kadsiyama, Japan by Ortmann.

A year later A. Milne Edwards & Bouvier (1893) examined two females collected by the "Blake" in the West Indian region and found them to represent two new species, which they described and assigned to *Anapagurus*, *A. acutus* and *A. marginatus*. In 1900 the same authors described *A. laevis* var. *longispina* (= *A. longispina*), and a questionable taxon *Anapagurus? dubius* (= *Acanthopagurus dubius*; see De Saint Laurent, 1968, 1969).

In two consecutive years Nobili (1905, 1906a) described respectively, *Anapagurus bonnieri* from the Persian Gulf, and *A. polynesiensis* (= *Micropagurus polynesiensis*; see Haig & Ball, 1988) from Rikitea, French Polynesia.

In the study of the hermit crabs of the Gulf of Naples, Fenizia (1937) described *A. breviaculeatus*, and ten years later Barnard (1947) added a South African species, *A. hendersoni*. The final three new taxa, prior to the present study, assigned to *Anapagurus* were described in the 1960s, *A. wolffi* Forest, 1961; *A. petiti* Dechancé & Forest, 1962; and *A. drachi* Forest, 1966. Table 1 summarizes this brief review of the literature on *Anapagurus* and shows the origins of several major taxonomic problems that exist in the genus.

Ingle (1985) proposed to reappraise the adult taxonomy of the pagurid hermit

Table 1. Summary of the history of the genus *Anapagurus* Henderson, 1886.

* <i>Anapagurus hyndmanni</i> (Bell, 1846)		
* <i>Anapagurus laevis</i> (Bell, 1846)		
* <i>Anapagurus chiroacanthus</i> (Lilljeborg, 1856)	←	(2)
<i>Anapagurus ferrugineus</i> (Norman, 1863)	← (1)	
* <i>Anapagurus pusillus</i> Henderson, 1888, sensu stricto		
<i>Anapagurus australiensis</i> Henderson, 1888 --- (3) ----→		<i>Micropagurus acantholepis</i> (Stimpson, 1858)
* <i>Anapagurus curvidactylus</i> Chevreux & Bouvier, 1892		
<i>Anapagurus brevicarpus</i> A. Milne Edwards & Bouvier, 1892		
* <i>Anapagurus bicorniger</i> A. Milne Edwards & Bouvier, 1892		
<i>Anapagurus pusillus</i> var. <i>japonica</i> Ortmann, 1892 -----→		* <i>Anapagurus japonicus</i>
<i>Anapagurus acutus</i> A. Milne Edwards & Bouvier, 1893 ----- (2) →		Species incertae sedis.
<i>Anapagurus marginatus</i> A. Milne Edwards & Bouvier, 1893 ----- (2) →		Species incertae sedis.
<i>Anapagurus laevis</i> var. <i>longispina</i> A. Milne Edwards & Bouvier, 1900 -----→		* <i>Anapagurus longispina</i>
<i>Anapagurus?</i> <i>dubius</i> A. Milne Edwards & Bouvier, 1900 ----- (4) →		<i>Acanthopagurus dubius</i>
* <i>Anapagurus bonnieri</i> Nobili, 1905		
<i>Anapagurus polynesiensis</i> Nobili, 1905 ----- (5) →		<i>Micropagurus polynesiensis</i>
* <i>Anapagurus breviaculeatus</i> Fenizia, 1937		
* <i>Anapagurus hendersoni</i> Barnard, 1947		
* <i>Anapagurus wolffi</i> Forest, 1961		
* <i>Anapagurus petiti</i> Dechancé & Forest, 1962		
<i>Anapagurus drachi</i> Forest, 1966 ----- (2) →		<i>Forestopagurus</i> gen. nov.
* <i>Anapagurus alboranensis</i> spec. nov.		
* <i>Anapagurus adriaticus</i> spec. nov.		
* <i>Anapagurus vossi</i> spec. nov.		
* <i>Anapagurus atlantidii</i> spec. nov.		
* <i>Anapagurus congolensis</i> spec. nov.		

References: (1) Norman, 1886: 7; (2) present study; (3) Gunn & McLaughlin, 1988: 68; (4) De Saint Laurent, 1969: 731; (5) Haig & Ball, 1988: 184.

\* Species presently assigned to *Anapagurus*

crabs occurring within the area of 30°N-80°N and 30°W-30°E in the northeastern Atlantic and the Mediterranean Sea. In this yet to be published work, Ingle intended to include those species of *Anapagurus* from this geographic area.

The objective of the present study is to do a worldwide revision of *Anapagurus* and to diagnose its species considering newly recognized characters, as well as the significance of intraspecific variation and interspecific overlap in morphological characters.

### Materials and methods

Due to the geographical distribution of *Anapagurus*, this study has been largely dependent on specimens from foreign museums, although some U.S. collections were also used. A total of 2473 specimens were examined, including *Anapagurus laevis* (204), *A. hyndmanni* (530), *A. chiroacanthus* (1005), *A. pusillus* (21), *A. japonicus* (2), *A. curvidactylus* (33), *A. bicorniger* (146), *A. longispina* (53), *A. bonnieri* (8), *A. breviaculeatus* (220), *A. hendersoni* (44), *A. wolffi* (6), *A. petiti* (59), *A. alboranensis* spec. nov. (27), *A. adriaticus* spec. nov. (75), *A. vossi* spec. nov. (11), *A. atlantidii* spec. nov. (6), and *A. congolensis* spec.

nov. (23). The material was borrowed and subsequently returned to the following institutions or private collections: British Museum (Natural History), London, England (BMNH); private collection of Carlo Frogia, Ancona, Italy (CF); Istituto di Ricerche sulla Pesca Marittima, Ancona, Italy (IRPEM); Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium (IRSNB-IG); Museum of Comparative Zoology, Harvard University, Massachusetts, U.S.A. (MCZ); Zoological Museum of the Moscow State University, Moscow, U.S.S.R. (MMSU); Museum National d'Histoire Naturelle, Paris, France (MNHN); Musée Océanographique, Monaco (MOM); Museo Civico di Storia Naturale, Milano, Italy (MSNM); Göteborgs Naturhistoriska Museum, Göteborg, Sweden (NHMG); Swedish Museum of Natural History, Stockholm, Sweden (NHRM); Indonesian National Institute of Oceanology, Jakarta, Indonesia (NIOJ); Osaka Museum of Natural History, Osaka, Japan (OMNH); Oxford University Museum, Oxford, England (OUM); Nationaal Natuurhistorisch Museum (formerly Rijksmuseum van Natuurlijke Historie), Leiden, Netherlands (RMNH); South African Museum, Cape Town, South Africa (SAM); Forschungsinstitut Natur Museum, Senckenberg, Germany (SMF); Zoological Museum, Tel-Aviv University, Tel-Aviv, Israel (TAU); Universidad de Málaga, Departamento de Zoología, Málaga, Spain (UMDZ); Rosenstiel School of Marine and Atmospheric Science, University of Miami, U.S.A. (UMML); National Museum of Natural History, Smithsonian Institution, Washington D.C., U.S.A. (USNM); Kumamoto University, Faculty of Education, Kumamoto, Japan (ZLKU); Museum für Naturkunde der Humboldt Universität zu Berlin, Germany (ZMB); and Zoologisk Museum, København, Denmark (ZMUC). Specimens examined in this study are listed by institutional acronym following Leviton et al. (1985) and Leviton & Gibbs (1988), with the exceptions of a few institutions that were not listed.

The specimens were examined using a Wild M-5 binocular stereomicroscope and the illustrations were prepared using a Wild M-5 drawing tube. The shield length (SL) has been measured from the tip of the rostrum to the midpoint of the posterior margin of the shield; measurements to the nearest 0.1 mm were made using an ocular micrometer. In the "Material" sections, shield lengths in millimeters are given in square brackets following the number of specimens. The number of specimens examined of the various species of *Anapagurus* and the range of shield length is presented in Table 2.

Detailed examination of the present extensive collections has made it possible to recognize reliable diagnostic characters and to evaluate the range of morphological variations. A separate section on "Morphological Considerations" has been included to describe diagnostically important structures and to clarify the terminology used. The systematic account includes: 1) synonymy and diagnosis of *Anapagurus*, 2) key to the species of *Anapagurus*, 3) complete synonymies and diagnoses of the 13 previously described species, 4) complete descriptions of the five new species, 5) detailed illustrations of all species, and 6) diagnosis of *Forestopagurus* gen. nov.

For each lot of specimens the following information is given: number of specimens arranged by sex, range of shield length, station number, collecting locality, depth of capture in meters (m), bottom type, date of collection, name of collector, and place of deposition. The material examined is arranged by geographic area and listed from north to south, and west to east. A distributional map is provided for each species showing the type locality and the present and recorded stations. The horizontal



Table 2. Number of specimens of *Anapagurus* examined in the present study and range of shield length (mm, in parentheses).

Species	all specimens combined	male	female		intersex	juvenile
			non-ovigerous	ovigerous		
<i>A. laevis</i>	204(1.0-6.0)	112(1.6-6.0)	31(1.2-3.9)	60(1.8-4.9)	-	1(1.0)
<i>A. hyndmanni</i>	530(1.0-5.0)	339(1.1-5.0)	49(1.2-3.9)	142(1.2-3.6)	-	-
<i>A. chiroacanthus</i>	1005(0.6-7.5)	506(0.6-3.0)	166(0.8-5.6)	309(0.8-3.2)	24(1.0-7.5)	-
<i>A. pusillus</i>	21(0.7-3.0)	6(1.2-2.6)	4(0.7-2.3)	11(0.9-3.0)	-	-
<i>A. japonicus</i>	2(1.3,1.9)	1(1.9)	1(1.3)	-	-	-
<i>A. curvidactylus</i>	33(0.8-2.1)	20(1.0-2.1)	2(0.8,1.9)	11(1.0-1.6)	-	-
<i>A. bicorniger</i>	146(1.2-6.0)	77(1.2-6.0)	15(1.4-2.7)	54(1.3-2.9)	-	-
<i>A. longispina</i>	53(1.2-2.8)	36(1.2-2.8)	8(1.6-2.7)	9(1.3-2.5)	-	-
<i>A. bonnieri</i>	8(1.2-2.0)	5(1.3-2.0)	-	3(1.2-1.7)	-	2(0.6)
<i>A. breviaculeatus</i>	220(0.6-3.7)	133(0.7-3.7)	32(0.8-2.9)	53(1.0-3.0)	-	-
<i>A. hendersoni</i>	44(1.1-3.5)	27(1.9-4.4)	6(1.1-3.3)	11(2.0-3.7)	-	-
<i>A. wolffi</i>	6(0.8-1.0)	2(0.8,1.0)	1(0.9)	3(0.9-1.0)	-	-
<i>A. petiti</i>	59(1.3-3.7)	32(1.3-3.7)	12(1.4-2.8)	15(1.8-3.3)	-	-
<i>A. alboranensis</i> spec. nov.	27(1.1-3.4)	21(1.5-2.9)	2(1.1,1.7)	4(2.0-3.4)	-	-
<i>A. adriaticus</i> spec. nov.	75(1.1-4.4)	44(1.3-4.4)	11(1.1-3.8)	20(1.6-4.0)	-	-
<i>A. vossi</i> spec. nov.	11(0.9-1.2)	8(0.9-1.5)	-	3(1.0-1.2)	-	-
<i>A. atlantidii</i> spec. nov.	6(0.9-1.5)	3(0.9-1.0)	-	3(1.3-1.5)	-	-
<i>A. congolensis</i> spec. nov.	23(1.8-3.4)	17(1.9-3.4)	3(2.2-2.3)	3(1.8-2.6)	-	-

Grand total 2473

and vertical distributions of the species are discussed in the section of "Biogeography". Information on the carcinoecia and symbiotic and other possible associations are given in separate sections of related organisms of each species account.

In the section "Related organisms" for each species of *Anapagurus* the number of specimens of the associated organism is provided besides the accession number or the acronym of the depository institution with the station number.

The symbols ♂ and ♀, and the abbreviation ovig., used in the sections on "Material" refer to male, non ovigerous, and ovigerous females, respectively. The abbreviation "AAK" stands for R/V "Academician A. Kovalevskii". The terminology applied to the lineae, sulci, and calcified areas of the cephalothorax follows in part that of Pilgrim (1973) and Morgan & Forest (1991).

### Morphological considerations

In general, the terminology for morphological structures follows that of McLaughlin (1974, 1980). However, it has been necessary to clarify the terminology and to describe several new diagnostically important structures.

The systematic confusion that has persisted among the species of *Anapagurus* can be attributed to inadequate diagnostic characters. There has been a tendency in the past to assign significant diagnostic importance to characters of the right cheliped. However, recent studies (McLaughlin, 1974; Lemaitre et al., 1982) have shown that the right cheliped in several genera of hermit crabs is affected by sexual dimorphism, age, environmental conditions, and type of carcinoecia used. The present studies

have shown that the right cheliped of species of *Anapagurus* has also been similarly influenced. Consequently interspecific overlaps in the ranges of related characters have occurred. Therefore, a combination of diagnostic characters must be used in separating the different species.

Species of three pagurid genera possess certain distinct projections between the ocular acicles, which are similar in their positions. In *Micropagurus acantholepis* (Stimpson, 1858) there are two lobular projections which have been called "bifurcated bracteole" by Stimpson (1907: 229) and "interocular lobes" (Gunn & McLaughlin (1988: 68, fig. 1a). In *Anapagurus bicorniger* and *A. petiti*, Dechancé & Forest (1962: 295, 297, figs. 1, 2) described two triangular lamellae which were called "sailles triangulaires interoculaires". While describing *Pagurus moluccensis*, Haig & Ball (1988: 187, fig. 14b) remarked on a "subrectangular interocular base with two elongate processes separated by deep, narrow median cleft". All these projections extend from the same structure that has been variously referred to as the "ophthalmic ring" (Stimpson, 1907), "anneau oculaire" (Bouvier, 1896, 1940), "ocular plate" (Snodgrass, 1951: 26, fig. 3E-e), and "ophthalmic somite" (Haig & Ball, 1988: 187); all of which imply that the structure is part of the eye. However, observing the molts, which give a more clear view of the head morphology, and following the opinion of McLaughlin (personal communication), I must conclude that the structure located between the ocular acicles does not constitute part of the eye. Dechancé & Forest (1962: 295) called the structure "la pièce interoculaire", which is more indicative of its location, and treated it as separate structure from the eye. Therefore the term "interocular plate" (fig. 1A) is adopted here and used throughout the text when referring to that structure.

Although slight variations were observed in the left chelipeds of species of *Anapagurus*, the considerable variations in the right chelipeds are taxonomically most important. The following new diagnostically important structures, which are apparently not affected by growth or sexual dimorphism, were found in the right chelipeds: (1) the shape and relative size of the mesial and lateral lobes that flank the dorsoproximal margin of palm (fig. 1B); (2) the shape and relative size of the median sinus of the ventroproximal palmar margin (fig. 1C); (3) the shape, armature and relative size of the dorsomesial distal carpal angle (fig. 1D); and (4) the shape and extension of both ventrodistal and ventroproximal carpal margins, which determine the relative ventral length (fig. 1C).

During this study other morphological characters, such as the relative length and setation of the ultimate antennular segment (fig. 1A), and the relative length between the right uropodal endopod and the distal protopodal lobe (fig. 1E), have been found to be of diagnostic significance.

### *Anapagurus* Henderson, 1886

*Spiropagurus* (*Anapagurus*) Henderson, 1886a: 337; 1886b: 73 (by implication; see remarks). Type species, by subsequent selection by Holthuis (1962: 242): *Pagurus laevis* Bell, 1846: 184.

*Anapagurus* Henderson, 1888: 73 (in part); Milne Edwards & Bouvier, 1893: 119 (in part).

**Diagnosis.**— Carapace with only shield well calcified. Anterior margin of shield slightly produced, rounded. Lateral projections with short submarginal spine, occasionally unarmed. Corneae dilated. Ocular acicles subtriangular to subovate, termi-

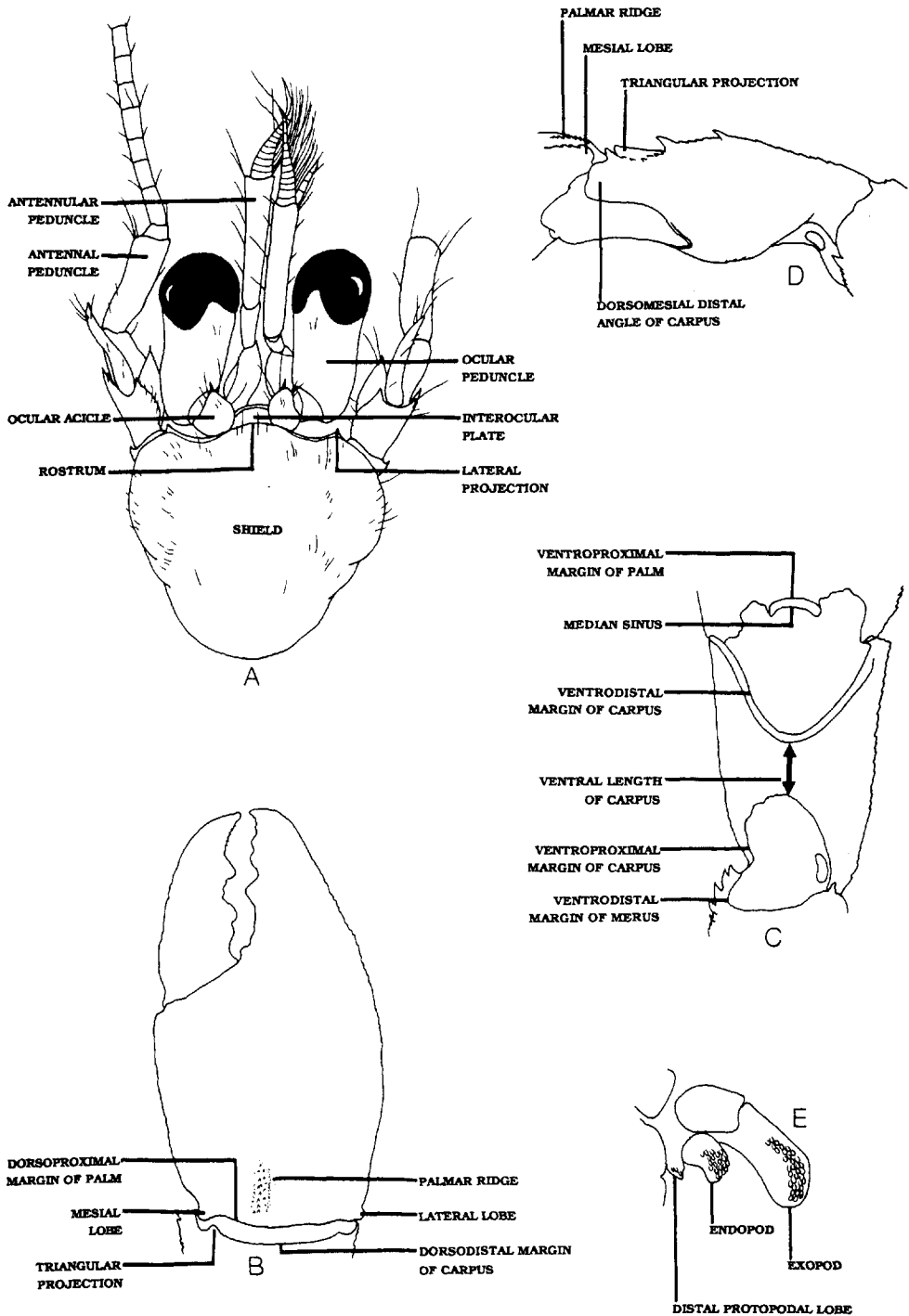


Fig. 1. Diagrammatic *Anapagurus*, showing terms used in text. A, shield and cephalic appendages; B-D, right cheliped: B, dorsal view of chela; C, ventral view of carpus; D, mesial view of carpus; E, dor-

nating in short submarginal, occasionally marginal spine. Interocular plate unarmed or with 2 chitinous spines. Antennal peduncle with supernumerary segmentation; acicle well-developed, slightly arcuate. Maxillule with stiff bristle on moderately well-developed internal endopodal lobe; external lobe lacking or weakly developed. Third maxilliped with 1 accessory tooth on well developed crista dentata. Sternite of 3rd maxillipeds leveled and with shallow median cleft. Eleven pairs of phyllobranchiae. Chelipeds unequal, right the larger; dactyls opening in horizontal plane. Ambulatory legs long and slender. Anterior lobe of sternite of third pereopods subrectangular. Fourth pereopods subchelate; dactyl without preungual process; propodal rasp with single row of closely spaced corneous scales. Sternite of 5th pereopods forming 2 widely spaced lobes. Males with coxa of left 5th pereopod somewhat enlarged and with well-developed, curved sexual tube; coxa of right 5th pereopod sometimes with short sexual tube, or occasionally with gonopore partly covered by tufts of long setae; with 3 unpaired pleopods. Females with paired gonopores; 4 unpaired pleopods, 2nd to 4th pleopods biramous, 5th uniramous. Uropods asymmetrical. Telson with transverse suture; posterior lobes asymmetrical, separated by median cleft; terminal margins each with 2 to 4 spines; lateral margins unarmed, occasionally each with 1 to 4 spinules.

Genus size.— Eighteen species are recognized here as belonging to *Anapagurus* Henderson, 1886. They are marked with an asterisk (\*) in Table 1.

Distribution.— With the exception of *Anapagurus bonnierii*, which has been collected in the Indian Ocean, and *A. japonicus* which lives in southern Japanese waters, the remaining 16 taxa of *Anapagurus* have an eastern Atlantic distribution, extending from the northwestern coast of Norway to the southern coast of South Africa. The depth range is 0-1262 m.

Remarks.— In the family Paguridae there are 22 genera with males having one or two sexual tubes (extruded vas deferens from the coxae of the 5th pereopods), highly advanced characteristics that easily separate them from other hermit crabs (Table 3).

Among the seven genera with well-developed, left sexual tubes, four were defined in part by the presence of an accessory tooth on the crista dentata of the 3rd maxilliped: *Spiropagurus* Stimpson, 1858; *Anapagurus* Henderson, 1886; *Micropagurus* McLaughlin, 1986; and *Pygmaeopagurus* McLaughlin, 1986; and three lack the accessory tooth, *Iridopagurus* De Saint Laurent-Dechancé, 1966; *Anapagrides* De Saint Laurent Dechancé, 1966; and *Enneobranchus* García-Gómez, 1988. A telson without a transverse suture, but with the terminal margin entire and multispinose ocular acicles immediately separates species of *Micropagurus* from species of *Spiropagurus*, *Anapagurus* and *Pygmaeopagurus*. The monotypic *Pygmaeopagurus*, represented by *P. hadrochirus* McLaughlin, is easily distinguished from species of *Spiropagurus* and *Anapagurus* by its massive right cheliped; ocular peduncles broad basally and tapering to bluntly pointed corneae; an obtusely triangular rostrum; and the absence of the male right gonopore. *Anapagurus* is distinguished from *Spiropagurus* by unequal chelipeds (the disparity in size is often very striking in adult males); more slender ambulatory legs with dactyls proportionately shorter and slightly setose; and, in males, a shorter curved left sexual tube.

*Anapagurus* was originally described by Henderson (1886a) as a subgenus of *Spiropagurus* when he listed its three species: *Spiropagurus* (*Anapagurus*) *hyndmanni*, *S. (A.) laevis*, and *S. (A.) ferrugineus*. In its appendix, Henderson noted that Norman

Table 3. Genera of the family Paguridae with males having sexual tubes.

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<i>Acanthopagurus</i> De Saint Laurent, 1968
<i>Anapagrides</i> De Saint Laurent, 1966
<i>Anapagurus</i> Henderson, 1886
<i>Catapaguroides</i> A. Milne Edwards & Bouvier, 1892
<i>Catapagurus</i> A. Milne Edwards, 1880
<i>Cestopagurus</i> Bouvier, 1897
<i>Decaphyllus</i> De Saint Laurent, 1968
<i>Enneobranchus</i> García-Gómez, 1988
<i>Forestopagurus</i> gen. nov.
<i>Goreopagurus</i> McLaughlin, 1986
<i>Iridopagurus</i> De Saint Laurent-Dechancé, 1966
<i>Micropagurus</i> McLaughlin, 1986
<i>Nanopagurus</i> McLaughlin, 1986
<i>Nematopaguroides</i> Forest & De Saint Laurent, 1967
<i>Nematopagurus</i> A. Milne Edwards & Bouvier, 1892
<i>Ostraconotus</i> A. Milne Edwards, 1880
<i>Pagurodes</i> Henderson, 1888
<i>Parapagurodes</i> McLaughlin & Haig, 1973
<i>Pygmaeopagurus</i> McLaughlin, 1986
<i>Solenopagurus</i> De Saint Laurent-Dechancé, 1968
<i>Spiropagurus</i> Stimpson, 1858
<i>Trichopagurus</i> De Saint Laurent, 1968

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(1886) had considered *Pagurus ferrugineus* a junior synonym of *Spiropagurus* (*Anapagurus*) *chiroacanthus*. Although in this paper and in a later publication (1886b) Henderson did not write explicitly *Spiropagurus* (*Anapagurus*), he made it clear that he considered *Anapagurus* a subgenus of *Spiropagurus*.

In 1893 A. Milne Edwards & Bouvier described *A. acutus* and *A. marginatus* based on two females collected in the tropical western Atlantic. Forest & De Saint Laurent (1967: 161) questioned the position of these species in *Anapagurus* and noted that their chelipeds resemble those of their newly erected *Nematopaguroides*. In the course of the present study, my examination of these two poorly preserved females and the descriptions and illustrations given by A. Milne Edwards & Bouvier (1893) have revealed important morphological differences in the armature of chelipeds and telson that exclude both species from *Anapagurus*. Both are herein considered species incertae sedis.

The study of the paratypes of *Anapagurus drachi* Forest, 1966 has revealed several important morphological differences (see under *Forestopagurus* gen. nov.: remarks) that set this species apart from *Anapagurus*, and a new genus is herein established for this taxon.

#### Key to the species of *Anapagurus*

1. Interocular plate with 2 chitinous spines ..... 2
- Interocular plate unarmed ..... 3
2. Antennal acicles unarmed. Carpus of right cheliped with 2 widely spaced spines on distal half of lateral face ..... *A. petiti* Dechancé & Forest, 1962

- Antennal acicles with short distal spine. Carpus of right cheliped without spines on lateral face ..... *A. bicorniger* A. Milne Edwards & Bouvier, 1892
- 3. Lateral margins of sternal lobes of 2nd pereopods parallel .....  
..... *A. hendersoni* Barnard, 1947
- Lateral margins of sternal lobes of 2nd pereopods convergent ..... 4
- 4. Ventrolateral distal angle of coxae of chelipeds with spines ..... 5
- Coxae of chelipeds with ventrolateral distal angle unarmed ..... 6
- 5. Right cheliped with spinulose ridge proximally near dorsomesial margin of palm; dorsomesial margin of carpus with row of 3 or 4 spines on distal half .....  
..... *A. atlantidii* spec. nov.
- Right cheliped without spinulose ridge proximally near dorsomesial margin of palm; dorsomesial margin of carpus with irregular row of closely spaced spines .... 7
- 6. Ocular acicles with marginal spine .....  
..... *A. longispina* A. Milne Edwards & Bouvier, 1900
- Ocular acicles with submarginal spine ..... 8
- 7. Dactyls of ambulatory legs with longitudinal sulci on lateral and mesial faces .....  
..... *A. hyndmanni* (Bell, 1846)
- Dactyls of ambulatory legs without longitudinal sulci .....  
..... *A. curvidactylus* Chevreux & Bouvier, 1892
- 8. Ultimate antennal segment not reaching base of corneae. Lateral projections of shield unarmed. Laterodistal margin of 1st antennal segment unarmed .....  
..... *A. wolffi* Forest, 1961
- Ultimate antennal segment reaching beyond base of corneae. Lateral projections of shield with short submarginal spine. Laterodistal margin of 1st antennal segment with short spine ..... 9
- 9. Dactyl of right chela with dorsomesial and ventrolateral ridges ..... 10
- Dactyl of right chela lacking ridges ..... 11
- 10. Dorsolateral margin of left cheliped spinose. Terminal margins of telson, each with 3 or 4 spines ..... *A. chiroacanthus* (Lilljeborg, 1856)
- Dorsolateral margin of left cheliped unarmed. Terminal margins of telson, each with 2 spines ..... *A. japonicus* Ortmann, 1892
- 11. Corneae dilated ..... 12
- Corneae not dilated ..... 13
- 12. Ultimate antennular segment with laterodistal tuft of 5-7 long setae. Terminal margins of telson, each with 2 or 3 spines and long submarginal stiff setae .....  
..... *A. vossi* spec. nov.
- Ultimate antennular segment with laterodistal tuft composed of 1 long and 1 or 2 short setae. Terminal margins of telson, each with 4 spines and very short submarginal stiff setae ..... 14
- 13. Lobes of sternite of 2nd pereopods with lateral spinules. Dorsomesial distal angle of carpus of right cheliped produced into subcircular lobe. Right cheliped of males at most with vestigial ventromesial meral protuberance .....  
..... *A. adriaticus* spec. nov.
- Lobes of sternite of 2nd pereopods unarmed. Dorsomesial distal angle of carpus of right cheliped produced into subtriangular or subrectangular lobe. Right cheliped of males with well- developed, ventromesial meral protuberance ..... 15

14. Ocular acicles ovate, mesial margins strongly expanded. Carpus of right cheliped with dorsomesial irregular row of spines. Lobes of sternite of 2nd pereopods latero-distally expanded ..... *A. laevis* (Bell, 1846)
- Ocular acicles roundly triangular, mesial margins not expanded. Carpus of right cheliped with dorsomesial row of strong spines on proximal  $\frac{4}{5}$ , and with 2 small spines distally. Lobes of sternite of 2nd pereopods not latero-distally expanded ...  
..... *A. congolensis* spec. nov.
15. Rostrum overreaching lateral projections. Dorsodistal margin of carpus of right cheliped lacking projection adjacent to dorsomesial distal angle .....  
..... *A. bonnieri* Nobili, 1905
- Rostrum exceeded by lateral projections. Dorsodistal margin of carpus of right cheliped with triangular or roundish projection adjacent to dorsomesial distal angle ..... 16
16. Shield broader than long. Ultimate antennular segment exceeding length of penultimate segment by  $\frac{1}{4}$  own length; ventral margin with row of tufts of long setae ..... *A. pusillus* Henderson, 1888
- Shield longer than broad. Ultimate antennular segment exceeding length of penultimate segment by  $\frac{1}{3}$  to  $\frac{1}{2}$  own length; ventral margin with row of tufts of very short setae ..... 17
17. Right cheliped with prominent, meral spinose protuberance in males .....  
..... *A. breviaculeatus* Fenizia, 1937
- Right cheliped with weakly developed, meral spinulose protuberance in males ...  
..... *A. alboranensis* spec. nov.

*Anapagurus laevis* (Bell, 1846)

(figs. 2, 3, 44g)

*Pagurus laevis* Thompson, 1844: 267, nomen nudum (see remarks).*Pagurus laevis* Bell, 1846: 184, 185, and unnumbered figure (see remarks); White, 1850: 26 (listed); Norman, 1861: 274; Carrington & Lovett, 1882: 391; Haddon & Shackleton, 1891: 637.*Eupagurus laevis*; Stimpson, 1858: 236 (listed); 1907: 216 (listed).*Spiropagurus laevis*; Norman, 1886: 7 (listed); Scott, 1888: 258 (listed); 1897: 172; Haddon & Shackleton, 1891: 637.*Spiropagurus* (*Anapagurus*) *laevis*; Henderson 1886a: 338; 1886b: 74 (by implication; see remarks for *Anapagurus*).*Anapagurus laevis*; Henderson, 1888: 73 (listed); Bouvier, 1891: 393, 394; 1896: 152; 1922: 31 (in part; see remarks); 1940: 145-147, fig. 100 bis, 107A; Chevreux & Bouvier, 1892b: 90, 91; A. Milne Edwards & Bouvier, 1892: 214 (in part); 1899: 66; 1900: 217, pl. XXVIII: figs. 9, 10 (in part; see remarks); Tattersall, 1905: 55; Norman, 1905: 8 (listed); Hansen, 1908: 29; Lagerberg, 1908: 62 (listed); Norman & Brady, 1911: 263; Patience, 1911: 74; Selbie, 1921: 44-48, pl. VII: figs. 7-9, pl. VIII: figs. 1-3; Balss, 1924: 768, 769 (listed); Nobre, 1931: 240, fig. 135; 1936: 148, pl. 49: fig. 125; Monod, 1932: 487 (listed); De Miranda y Rivera, 1933: 30, 60 (listed); Dollfus & Carayon, 1942: 445, figs. 1-4; Calgren, 1945: 77; Thorson, 1946: 340; Zariquiey Alvarez, 1946: 122, 123, fig. 157; 1955: 402; 1968: 256, 257, figs. 90r, 91j; Holthuis, 1950: 139-141, fig. 50; 1962: 242 (type species by subsequent selection, *Pagurus laevis* Bell, 1846); Pike, 1953: 226, 227, 230; 1961: 226, 227, 229, 230, 232, 233, 237-239, figs. 2B, 4, 7B; Forest, 1958: 100 (see remarks); 1965: 355, 356, figs. 12, 14, 15, 20; Gordan, 1956: 303 (listed); MacDonald, Pike & Williamson, 1957: 237-240, fig. 8; Füller, 1958: 164; Pike & Williamson, 1958: 6-8, figs. 26-29; 1959: 562, 563, fig. 4; 1960: 525; Dechancé & Dufaure, 1959: 1566-1568; Peres & Picard, 1964: 104; Ross, 1967: 306 (listed); Bourdon, 1968: 195; Hazlett, 1968a: 138; 1968b: 248; Gilpin-Brown, 1969:

126; Gilat, 1969: 16, 54; Nielsen, 1970: 19, fig. 2A-D; Guille, 1971: 132; Naylor, 1972: 70, 78; Jensen & Bender, 1973: 190 (listed); Türkay, 1976: 36 (in part; see remarks); Neves, 1977: 179, 180; Manuel, 1981: 73; García Raso, 1982: 501, 502; Matallanas, 1982: 248, 250, 251; Cranmer, Dyer & Fry, 1984: 342 (listed); Ingle, 1985: 764 (listed); Peres, 1985: 211, 225; Høeg & Lutzen, 1985: 36, 41; Lindley, 1986: 546, 548; Muirhead, Tyler & Thurston, 1986: 131; Markham, 1986: 154; Riedl, 1986: 498, pl. 178: unnumbered figure; Basford, Eleftheriou, & Raffaelli, 1989: 400.

*Anapagurus loevis*; A. Milne Edwards & Bouvier, 1894: 72, pl. XI: figs. 16-28 (in part; see remarks)(misspelling of *A. laevis*).

? *Anapagurus laevis*; Balss, 1926: 375, 377, 379; 1957: 1751; Mouchet, 1931: 14, 88-90, figs. 85, 86; Lewinsohn, 1976: 245, 246; Shiber & Fattah, 1978: 131 (listed); Kocatas, 1981: 162; Doumenc, Chintiroglou & Koukouras, 1985: 517 (see remarks).

? *Anapagurus levis*; Fenizia, 1937: text and figure legends for figs. 15, 16 (misspelling of *A. laevis*).

not *Anapagurus laevis*; Forest, 1955: 131, 132, fig. 31, pl. VI: fig. 6 (= *A. congolensis* spec. nov.; fig. 32, pl. VI: figs. 7, 8 (= *A. hendersoni* Barnard, 1947) (see remarks).

not *Anapagurus laevis*; Forest, 1961: 239 (= *A. wolffi* Forest, 1961; *A. vossi* spec. nov.); figs. 8, 12, 16 (= *A. atlantidii* spec. nov.)

not ? *Anapagurus laevis*; Holthuis & Gottlieb, 1958: 72 (see remarks).

? not *Anapagurus laevis*; Fenizia, 1937: 22-24, figs. 15, 16; Sarojini & Nagabushanam, 1969: 387, 388.

**Material.**— Syntypes: OUM; not examined. **Northeastern Atlantic: Norway:** 8 ♂♂ [2.8-4.5], 9 ovig. [2.6-3.6], Excursion RMNH station 5, 63°42'N, 9°51'E, 35-50 m, 20.viii.1963, RMNH D 20254; 3 ♂♂ [2.0-3.9], 3 ♀♀ [2.6-3.9], Excursion RMNH station 7, 63°42'N, 9°55'E, 50 m, 20.viii.1963, RMNH D 20255; 1 ovig. [2.1], Excursion RMNH station 17, 63°41'N, 9°21'E, 90 m, 23.viii.1963, RMNH D 20261; 1 ♀ [3.0], Excursion RMNH, 63°39'N, 9°30'E, 5-10 m, 31.viii.1961, RMNH D 17519; 1 ovig. [2.6], Excursion RMNH station 127, 63°41'N, 9°42'E, 25-50 m, RMNH D 24217; 1 ovig. [4.2], Excursion RMNH station 105, 63°43'N, 9°53'E, 150-200 m, 24.viii.1965, RMNH D 24218; 1 ♂ [3.9], Scandinavian Excursion station 7, Stjørnfjord, 20.viii.1963, RMNH D 24219; 1 ♀ [2.9], Molde Fjord, collector Schottländer, ZMB 20266; 2 ovig. [2.7, 3.4], off Bergen, viii.1907, collector Utrecht, RMNH D 4831; 1 ovig. [4.9], station 1225, off Storeggen, collector Uddström, NHRM 1179; 1 ♂ [5.9], station 1227, off Storeggen, collector Uddström, NHRM 1181; 1 ovig. [3.9], off Bergen, 182.9-292.6 m, 1877, collector O. Johanson, NHRM 2082; 1 ovig. [4.3], station L 369, off Bergen, 182.9-219.5 m, 1877, collector M. Olsson, NHRM 2084; 1 ovig. [4.7], off Bergen, 164.6-292.6 m, 1880, collector G. Nilsson, NHRM 2419; 2 ♂♂ [5.1, 6.0], 2 ovig. [2.9, 3.8], station L763, off Bergen, 274.3 m, 1880, collector T. Anderson, NHRM 2449; 1 ovig. [4.1], station L763, off Sorfjord, 36.6 m, vii.1880, collector Bovallius, NHRM 2472; 1 ♂ [3.4], 1 ovig. [3.1], off Storeggen, 109.7-128.0 m, NHRM 1444; 1 ♂ [3.5], station 1766, off Godö, 164.6 m, 1867, collector V. Yhlen, NHRM 1507; 1 ovig. [2.8], station 1767, off Rondö, 109.7 m, 1867, collector V. Yhlen, NHRM 1508; 1 ♂ [1.7], station 1771, off Jederen, 457.2 m, sandy bottom, 1867, collector V. Yhlen, NHRM 1512; 1 ovig. [2.9], station 1772, off Jederen, 457.2 m, sandy bottom, 1867, collector V. Yhlen, NHRM 1513; 1 ♀ [2.3], station 1775, off Jederen, 457.2 m, sandy bottom, 1867, collector V. Yhlen, NHRM 1516; 1 ovig. [2.4], station 1777, off Bodypet, 36.6 m, 1867, collector V. Yhlen, NHRM 1518; 1 ovig. [3.5], station 1776, off Sukkertoppen, 109.7 m, 1867, NHRM 1520; 1 ♀ [2.1], station 2284, off Storeggen, 128 m, rocky bottom, 1867, NHRM 2009; 6 ♂♂ [1.9-3.8], 3 ♀♀ [2.2-2.4], 1 ovig. [2.9], Excursion RMNH, 59°15.5'N, 5°11'E, 30-35 m, 9.ix.1961, RMNH D 17520; 1 ♂ [4.4], 3 ovig. [2.6-3.3], 1884, collector A.M.Norman, USNM 6809. **Sweden:** juvenile [1.0], station 1224, off Väderöarna, collector Goës, NHRM 1178; 1 ♂ [3.6], off Gäsö ränna, vi.1913, NHRM 4378; 1 ovig. [2.8], Kristinebergs Zoological Station, off Väderöarna, 20 m, bottom of rocks and gravel, 7.vii.1926, NHRM 4646; 1 ♂ [3.1], off Väderöarna, coralline bottom, 3.vii.1930, collector S. Bock, NHRM 5172; 1 ♂ [2.7], off Kummelbanken, 1900, collector T. Tullberg, NHRM 4173. **Denmark:** Kattegat: 1 ovig. [3.7], "Hauch" station 58, ca. 57°45'N, ca. 10°45'E, 132 m, fine clay with fine sand, 19.viii.1884, ZMUC; 1 ovig. [3.9], "Hauch" station 239, ca. 57°10'N, ca. 11°40'E, 55 m, fine clay with coarse sand, 21.viii.1885, ZMUC; 1 ♂ [4.0], "Hauch" station 243, ca. 57°05'N, ca. 11°40'E, 43 m, gravels with little clay, 24.viii.1885, ZMUC; 1 ovig. [4.0], "Hauch" station 474, ca. 57°05'N, ca. 11°40'E, 44 m, a little clay, 23.viii.1886, ZMUC. **British Isles:** 2 ♂♂ [2.5, 3.0], station 1226, off Nordsjön, Shetland Islands, collector Verngren, NHRM 1180; 1 ♂ [4.6], 1 ovig. [2.8], "N.L. Grönlands Expedition



1889", 61°16'N, 1°18'W, 150 m, bottom of sand, stones, and shells, 31.v.1889, NHRM 3930; 1 ♂ [4.2], 2 ovig. [2.8, 3.1], off Nordsjon, Shetland Islands, collector A.M. Norman, NHRM 6889; 2 ♂♂ [4.4, 4.7], 2 ovig. [2.7, 3.0], off Shetland Islands, collector A.M. Norman, USNM 17006; 4 ♂♂ [2.0-4.0], 2 ovig. [2.1], "Princesse Alice II" station 1043, 59°03'N, 1°47'45"W, 88 m, 13.ix.1898, MOM 380727; 2 ♀♀ [2.0, 2.2], station 101, 58°56'N, 1°21'W, 115 m, 27.vi.1908, RMNH D 29773; 1 ♂ [4.2], "Deutsche Tiefsee Expedition" station 3, off Aberdeen, 5.viii.1898, ZMB 16477; 6 ♂♂ [2.8-3.9], 1 ♀ [2.8], 1 ovig. [3.6], off Plymouth, MSNM 1870; 1 ♂ [3.4], 2 ♀♀ [3.2, 3.5], off Plymouth, MSNM 2074; 1 ♀ [3.3], off Plymouth, ZMUC; 25 ♂♂ [2.5-4.4], 1 ♀ [3.2], 10 ovig. [2.5-4.0], Firth of Clyde, collector J. Murray, USNM 16991. **Bay of Biscay:** 1 ♂ [1.6], 1 ♀ [1.2], "Hirondelle" station 42, 46°47'N, 6°12'30"W, 136 m, bottom of fine sand, 18.vii.1886, MOM 380021; 1 ♀ [1.4], "Hirondelle" station 44, 46°27'N, 6°30'W, 166 m, silty sand bottom, 20.vii.1886, MOM 380033; 8 ♂♂ [2.1-3.2], 2 ♀♀ [2.1, 2.2], "Hirondelle" station 45, 45°48'N, 5°58'W, 160 m, bottom of fine sand, 21.vii.1886, MOM 380042; 1 ♂ [2.4], 3 ♀♀ [2.6-3.9] "Hirondelle" station 46, 46°24'42"N, 5°55'30"W, 155 m, bottom of gray sand, 26.vii.1886, MOM 380054; 3 ♂♂ [1.6-2.7], 1 ♀ [2.2], "Hirondelle" station 85, 46°31'N, 6°52'W, 180 m, silty sand bottom, 28.v.1887, MOM 380118; 1 ♂ [2.7], "Princesse Alice" station 503, from 47°10'N, 8°08'W to 47°12'N, 8°12'W, 1262-748 m, bottom of clay and silty sand, 29.viii.1894, MOM 380271; 1 ovig. [3.0], "Princesse Alice II" station 1463, from 45°20'N, 3°17'W to 45°24'N, 3°07'W, 950-150 m, 27.vii.1902, MOM 380881; 1 ♀ [2.4], "Hirondelle" station 57, 43°44'30"N, 8°32'30"W, 240 m, bottom of rocks, pebbles, and sand, 5.viii.1886, MOM 382509; 4 ♂♂ [2.8-4.0], 1 ♀ [3.0], station 346, 43°51.0'N, 02°11.9'W, 460-520 m, 3.x.1970, MNHN 1995. **Spain:** 1 ♂ [1.8], Excursion RMNH station 1.157, off Isla Jidoiro, Ría de Arosa, 42 m, 30.vii.1962, RMNH D 19364; 3 ♂♂ [2.0-3.1], 1 ovig. [2.8], Excursion RMNH station 1.418, off Punta Figueiriño, Isla Salvora, Ría de Arosa, 50 m, 13.vii.1963, RMNH D; 1 ♀ [2.5], Excursion RMNH station 1.415, off Punta Figueiriño, Isla Salvora, Ría de Arosa, 50-54 m, 13.vii.1963, RMNH D 20260; 1 ♂ [3.8], 1 ♀ [2.1], Excursion RMNH station 1.417, off Punta Porto Chunco, Península del Grove, Ría de Arosa, 27 m, 23.vii.1963, RMNH D; 1 ovig. [2.1], Excursion RMNH station 1.349, off Punta Barbafeitas, Isla de Arosa, Ría de Arosa, 45 m, 9.vii.1963, RMNH D 20256; 1 ♀ [2.1], "Josefa Cambeira" station 1.841, 42°26.5'N, 08°57.3'W, 35-65 m, 6.viii.1964, collector L.B. Holthuis, USNM 121796; 1 ♂ [3.4], "Josefa Cambeira" station 1.722, 42°33.0'N, 08°55.5'W, 70-50 m, collector L.B. Holthuis, USNM 121795; 1 ovig. [2.9], "Josefa Cambeira" station 121794, 42°30.4'N, 08°56.2'W, 45 m, collector L.B. Holthuis, USNM 121794; 1 ♀ [2.2], Excursion RMNH station 1.187, off Punta del Castillo, Ría de Arosa, 11 m, sandy bottom, 1.viii.1962, RMNH D 18599; 1 ♂ [3.4], "Josefa Cambeira" station 1.842, off Punta del Castillo, Isla Salvora, Ría de Arosa, 45-55 m, 2 ♂♂ [2.9, 3.6], 1 ♀ [2.7], "Josefa Cambeira" station 1.898, off Light Loba de Cordeiro, Ría de Arosa, 35-45 m, 11.viii.1964, RMNH D 24221. **Portugal:** 1 ♂ [1.9], 2 ovig. [1.8], 39°17'N, 9°30'W, 66 m, 2.ix.1951, collector K.W. Schuitema, RMNH D 7979; 1 ♂ [1.6], "Meteor" station 9c90, 37°14.7'N, 9°1.5'W, 114-117 m, 22.vi.1967, collector Thiel, SMF 4799; 3 ♂♂ [2.5-3.6], "Talisman" 39°53'N, 10°52'W, 99 m, bottom of silt and shells, 6.vi.1883, MCZ 6580; 1 ♂ [2.5], "Talisman", 39°53'N 10°52'W, 99 m, bottom of silt and shells, 6.vi.1883, USNM 22922. **Mediterranean Sea: Spain:** 2 ♂♂ [3.4, 3.8], off Málaga, 35-43 m, 1979, collector J.E. García Raso, UMDZ. **France:** 1 ♂ [3.0], station 40, off Beaulieu, 30 m, MOM 382511. **Monaco:** 1 ♂ [3.1], 1 ♀ [3.3], 1 ovig. [2.4], "Navire Eider", 50 m off Bas Moulins, 15 m, 17.ii.1909, collector Gangui, MOM 382512. **Off Mauritania:** 1 ♂ [2.3], "Tyde-man" station 3.116, off Cap Blanc, 20°20'N, 17°42'W, 105 m, 27.x.1978, RMNH D. **Uncertain localities:** 1 ♂ [3.5], 1 ovig. [3.0], By Fjord, 29.ix.1907, collector C. Sopta, RMNH D 3712; 1 ♂ [3.6], "Thor" station 284, off NW Thagras Fyrshite, 90 m, 13.x.1904, ZMUC.

**Diagnosis.**— Shield broader than long. Rostrum slightly exceeded by lateral projections. Lateral projections with short submarginal spine.

Ocular peduncles approximately  $\frac{3}{5}$  length of shield; with corneae strongly dilated. Ocular acicles ovate with mesiodistal margins strongly expanded, with short, submarginal spine. Interocular plate unarmed.

Antennular peduncles exceeding distal margin of corneae by approximately entire length of ultimate segment. Ultimate segment exceeding length of penultimate segment by approximately  $\frac{1}{3}$  own length, with dorsolateral row of tufts of short

setae and 2 distal setae, 1 moderately long, 1 short; dorsomesial and ventral margins each with row of tufts of moderately long setae; basal segment with long, lateromedial spine and 1 short, ventromesial, distal spine.

Antennal peduncles overreaching corneae distally by approximately  $\frac{2}{3}$  length of ultimate segment. Antennal acicles terminating in small spine, usually overreaching corneae distally.

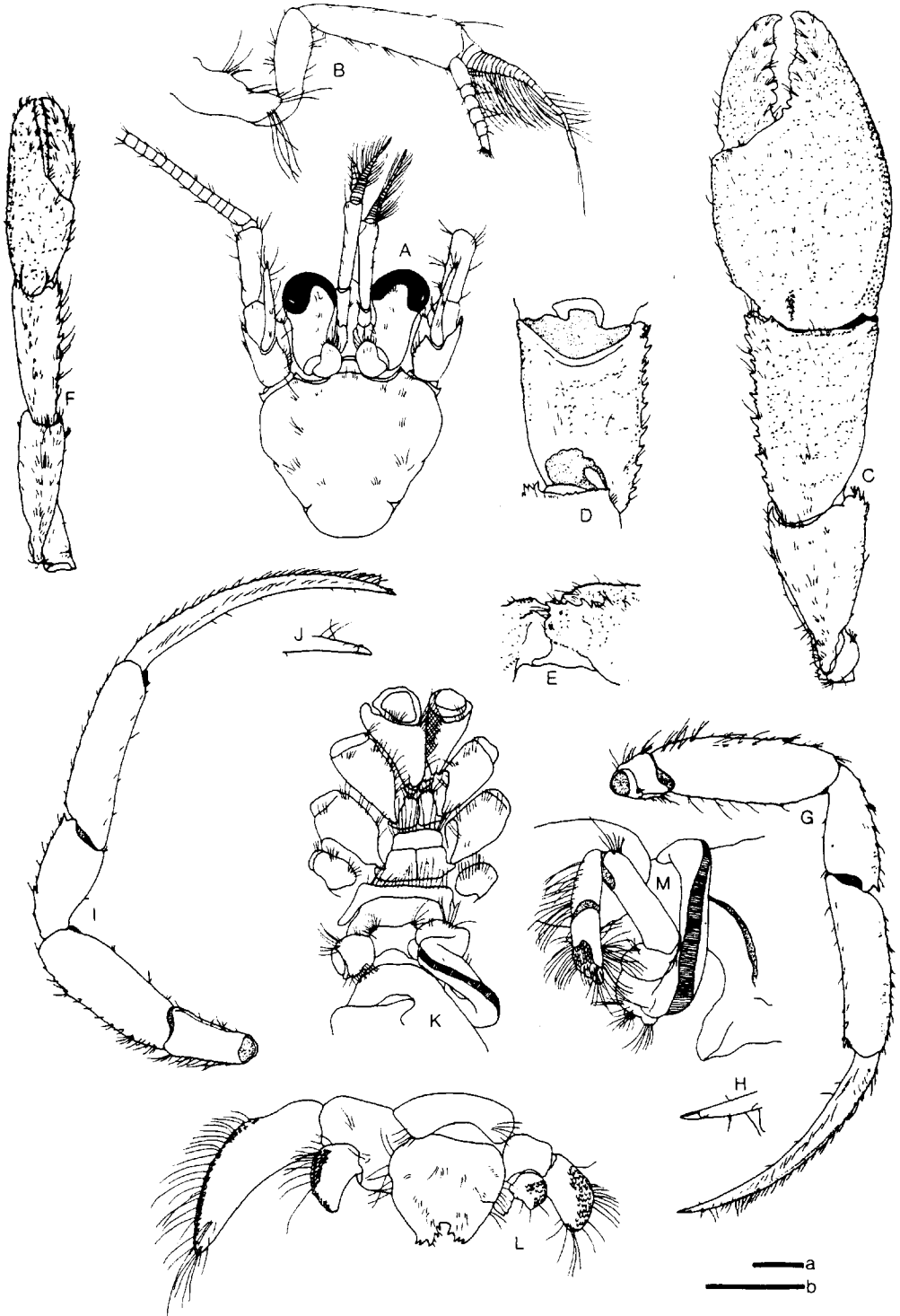
Right cheliped with moderately narrow chela. Dactyl approximately  $\frac{3}{4}$  length of palm, slightly curved ventrally; subcircular in cross section, with no ridges. Palm subequal to length of carpus, dorsomesial margin with spinulose ridge on proximal half; dorsal surface convex, with scattered granules or spinules and short setae, prominent, spinulose ridge near dorsomesial margin proximally; dorsolateral margin with spinules extending onto fixed finger and becoming obsolete near claw; dorso-proximal margin with well-developed lobes, laterally and mesially, larger mesial lobe with marginal spinules; ventroproximal margin with skewed, median, subquadrate sinus. Carpus exceeding length of merus by approximately  $\frac{1}{4}$  own length; dorsomesial margin with row of spines of different sizes; dorsomesial, distal angle produced into concave, large subrectangular structure, with more raised, ventral, spinulose side; dorsodistal margin with strong, raised, triangular projection adjacent to dorsomesial, distal angle; dorsolateral margin with 1 short spine on proximal third; ventral surface inflated with tufts of short, stiff setae; ventromesial margin subcircular in mesial view; moderately long, ventral length between shallow, subtriangular, ventrodistal and shallow, subcircular, ventroproximal margins. Ventromesial margin of merus with spinules and 1 short, distal spine; ventrolateral margin with 3 to 5 long spines; dorsal margin with short, distal spine. Coxae of chelipeds with ventrolateral, distal angle unarmed.

Dactyl of left cheliped granulose or spinulose and tufts of moderately long setae. Dorsomesial margin of carpus with row of 7 to 11 strong, closely spaced spines increasing in size distally; dorsolateral margin with row of 3 to 6 short, closely spaced spines on proximal half and row of spinules distally.

Dactyls of ambulatory legs exceeding length of propodi by approximately  $\frac{1}{4}$  own length, with dorsomesial and ventromesial rows of closely spaced, moderately long setae. Propodi exceeding length of carpi by approximately  $\frac{1}{3}$  own length; ventromesial, distal angle with corneous spines, 1-3 short (2nd), 1 very short or unarmed (3rd). Carpi  $\frac{2}{3}$  length of meri; dorsal margins with row of short spines (2nd) or with 1 proximal and 1 distal spine (3rd). Meri with 1 spinule on distal third, dorsally (2nd, 3rd) and ventrally (2nd). Lobes of sternite of 2nd pereopods unarmed, laterodistally expanded. Anterior lobe of sternite of 3rd pereopods subrectangular, with well-defined, distal angles.

Males with moderately long and broad, left sexual tube, smoothly recurved distally, and conical short, backwardly directed right sexual tube; pleopods 3 and 4

Fig. 2. *Anapagurus laevis* (Bell, 1846). ♂ (4.0 mm), "Thor" station 243, of Thagras Fyrshite, ZMUC: A, shield and cephalic appendages; B, left antennule (lateral view); C, right cheliped (dorsal view); D, carpus of same (ventral view); E, joint of palm and carpus of same (mesial view); F, left cheliped (dorsal view); G, left 2nd pereopod (mesial view); H, tip of dactyl of same; I, left 3rd pereopod (mesial view); J, tip of dactyl of same; K, sternum; L, extremity of abdomen, uropods and telson; M, left sexual tube (lateral view). Scales equal 1.0 mm: a: A, C-G, I, K, M; b: B, H, J, L.



unequally biramous, pleopod 5 uniramous. Right, distal protopodal lobe approximately  $\frac{1}{2}$  length of uropodal endopod. Telson with posterior asymmetrical lobes, separated by narrow, moderately deep cleft; terminal margins each with 4 short spines; lateral margins with moderately long setae, unarmed, occasionally with 1 spinule.

Colour.—“The general colour is yellowish testaceous, and there is a distinct red mark extending the whole length of the hand and bifurcating towards the fingers” (Bell, 1846).

Behaviour.—Hazlett studied the dislodging (1968a) and sexual (1968b) behaviour of *A. laevis*.

Related organisms.—The following gastropod and scaphopod shells occupied by *A. laevis* have been reported: *Natica*, *Murex*, *Dentalium* by Carrington & Lovett (1982); *Turritella* (6 specimens), *Nasse* (= *Hinia*), *Trochus*, *Murex*, and *Natice* (= *Natica*) by A. Milne Edwards & Bouvier (1900); *Natica nitida* by Dollfus & Carayon (1942); and *Turritella communis* Risso by Pike & Williamson (1959). In the present collections the following shells inhabited by *A. laevis* have been found: *Buccinum humphreysianum* Bennett, 1825 (1 specimen, RMNH D 20256); *Buccinum undatum* Linnaeus (3 specimens: USNM 16991, ZMUC station 243, and “Thor” station 284); *Colus jeffreysianus* (Fischer) (1 specimen, NHRM 3930); *Gibbula divaricata* Linnaeus (1 specimen, USNM 16991); *Hinia reticulata* (Linnaeus) (1 specimen, NHRM 2472); *Littorina littorea* Linnaeus (2 specimens, USNM 16991); *Lunatia guillemini* (Payraudeau) (1 specimen, USNM 16991); *Natica catena* da Costa (3 specimens: RMNH D 3712, NHRM 1518, and NHRM 4649); *Polinices grossularius* Marche Marchad, 1957 (1 specimen, RMNH D “Tydeman” 27.x.1978); Turridae (1 specimen, ZMB 20266); *Turritella biplicata* (Bronn) (2 specimens: RMNH D 3712 and RMNH D 7979); *Turritella communis* (11 specimens: MSNM 1870, MSNM 2074, RMNH D 4831, NHRM 3930, USNM 16991, and ZMUC-20.xi.1922); and unidentified shell (NHRM 1180).

The following organisms found attached outside shells inhabited by *A. laevis* have been reported: Cnidaria: *Epizoanthus incrustatus* Duben & Koren, 1847: [Haddon & Shackleton, 1891; Balss, 1924 (listed); Carlgren, 1945; Füller, 1958 (listed); Jensen & Bender 1973 (listed); Manuel, 1981; Cranmer, Dyer & Fry, 1984 (listed); and Muirhead, Tyler & Thurston, 1986].—*Paracalliactis lacazei* Dechancé & Dufaure, 1959: new species collected off Banyuls-sur-Mer.—? *Adamsia palliata* (Boahadsch, 1761): Doumenc, Chintiroglou & Koukouras, 1985 (Aegean Sea). Polychaete *Nereis fucata* (Savigny): Pike & Williamson, 1952; Gilpin-Brown, 1969. In the present collections a number of specimens of *A. laevis* (in parentheses) have been found in shells incrustated by the following organisms: Cnidarian *Epizoanthus incrustatus*: (1) RMNH D 29773 and (1) NHRM 2449. Poriferan *Suberites domuncula* (Olivi): (1) RMNH D 29773 (new record). Serpulid polychaetes: (1) NHRM 3930; (8) USNM 16991; and (1) ZMUC-20.xi.1922. Cirripedian *Balanus* sp: (1) USNM 16991.

*Anapagurus laevis* has been reported as a host for the following parasites: Isopoda: *Athelges paguri* Rathke: Tattersall, 1905; Patience, 1911; Pike, 1953 and 1961; Naylor, 1972; *Pseudione hyndmanni* Bate & Westwood, 1868: Dollfus & Carayon, 1942; Pike, 1953 and 1961; Bourdon, 1968; Markham, 1986 (listed); *Liriopsis pygmaea* Rathke (hyperparasite on *Peltogaster paguri* infesting *A. laevis*): Pike, 1961; Ross, 1967 (listed); Naylor, 1972. Cirripedia: *Peltogaster paguri* Rathke, 1842: Nielsen, 1970; Høeg & Lutzen, 1985; *Peltogasterella sulcata* (Lilljeborg, 1859): Nielsen, 1970 (as *Gemmosaccus sul-*

*catus*); Høeg & Lutzen, 1985. In the present collections the following parasites infesting *A. laevis* have been found: Isopoda: *Pseudione hyndmanni* in right branchial chamber of a male collected off N.W. Thagras Fyrshite, "Thor" station 284, ZMUC; no external effects of the parasitism were observed. Cirripedia: *Peltogaster paguri* (1 externa per host): 1 male lacking left sexual tube and pleopod 4 and another male with no external effects (RMNH D 20254); 1 female with reduced pleopods 2, 3, lacking pleopod 4 (RMNH D 20255); 1 male with short left sexual tube, lacking pleopod 3 (NHRM 1507); 1 male lacking left sexual tube and pleopod 4, reduced pleopod 3 (USNM 16991); *Peltogasterella sulcata* (9 externae per host): 1 male with short left sexual tube, feminization of pleopods (MSNM 1870).

The following organisms were found attached to different parts of specimens of *A. laevis*: Serpulid polychaetes: dorsally on carpus of right cheliped (NHRM 3930); ventrally on palm and carpus of right cheliped (USNM 17006). Foraminifera: 2 tests on shield, and 1 dorsally on propodous of right 2nd pereopod (NHRM 1516); 6 tests dorsally on right cheliped: 4 on palm and 2 on carpus (USNM 17006); 1 test dorsally on carpus of right cheliped (USNM 121794). Bryozoa: 1 colony middorsally on palm of right cheliped (USNM 17006). Matallanas (1982) found *A. laevis* the most abundant organism in the stomach of the fish *Macroramphosus scolopax* (Linnaeus) collected off the Catalan coast of Spain.

Life history.— Mouchet (1931) described and illustrated the spermatophores presumable of *A. laevis* from specimens collected off Salammbô, Tunisia. Thorson (1946) covered the breeding and reproduction aspects of this species. The zoeal stages and glaucothoe of *A. laevis* have been described by MacDonald, Pike & Williamson (1957), and Pike & Williamson (1958, 1960). Lindley (1986) reported the vertical larval distribution of *A. laevis* in the Great Sole Bank, Celtic Sea.

Distribution.— *Anapagurus laevis* has been collected in the eastern Atlantic from off Trondheimsfjord, 63°43'N, 9°53'E, Norway to off Mauritania, 17°02'N, 18°59'W, (Chevreux & Bouvier, 1892). The occurrence of *A. laevis* is herein confirmed in the western Mediterranean (i.e., Spain, France, Monaco) and questionably reported from the eastern Mediterranean. References of *A. laevis* off Naples (Balss, 1926; Fenizia, 1937), Adriatic Sea (Balss, 1957), Aegean Sea (Kocatas, 1981; Doumenc, Chintiroglou & Koukouras, 1985), and off Salammbô, Tunisia (Mouchet, 1931) are questionably assigned to Bell's taxon (see remarks). Depth range: 4.6 (Hansen, 1908)-1262 m (*A. Milne Edwards & Bouvier*, 1899); most frequently found in depths of 20 to 200 m.

Affinities.— Though *Anapagurus laevis* is most closely allied to *A. vossi* spec. nov. and *A. congolensis* spec. nov., also shares the overall appearance and armature of *A. adriaticus* spec. nov. (see section on affinities for *A. adriaticus* spec. nov.). The relationship between Bell's taxon and the two new taxa is inferred from the similarity observed between small adults of comparable size. These three taxa share among others, the following characters, e.g., the strongly dilated corneae and the much broader than long shield. The ultimate antennular segment with laterodistal tufts of fewer (2 or 3) setae, the dorsomesial distal spine of carpus of right cheliped with the same inclination (approximately 45°) as the other dorsomesial spines, and the distal armature of telson with short, submarginal, stiff setae easily distinguish *A. laevis* from *A. vossi* spec. nov. *Anapagurus laevis* can be separated from *A. congolensis* spec. nov., by the former's ovate ocular acicles with mesial margins strongly expanded, carpus of right cheliped with dorsomesial row of spines of different sizes, lobes of

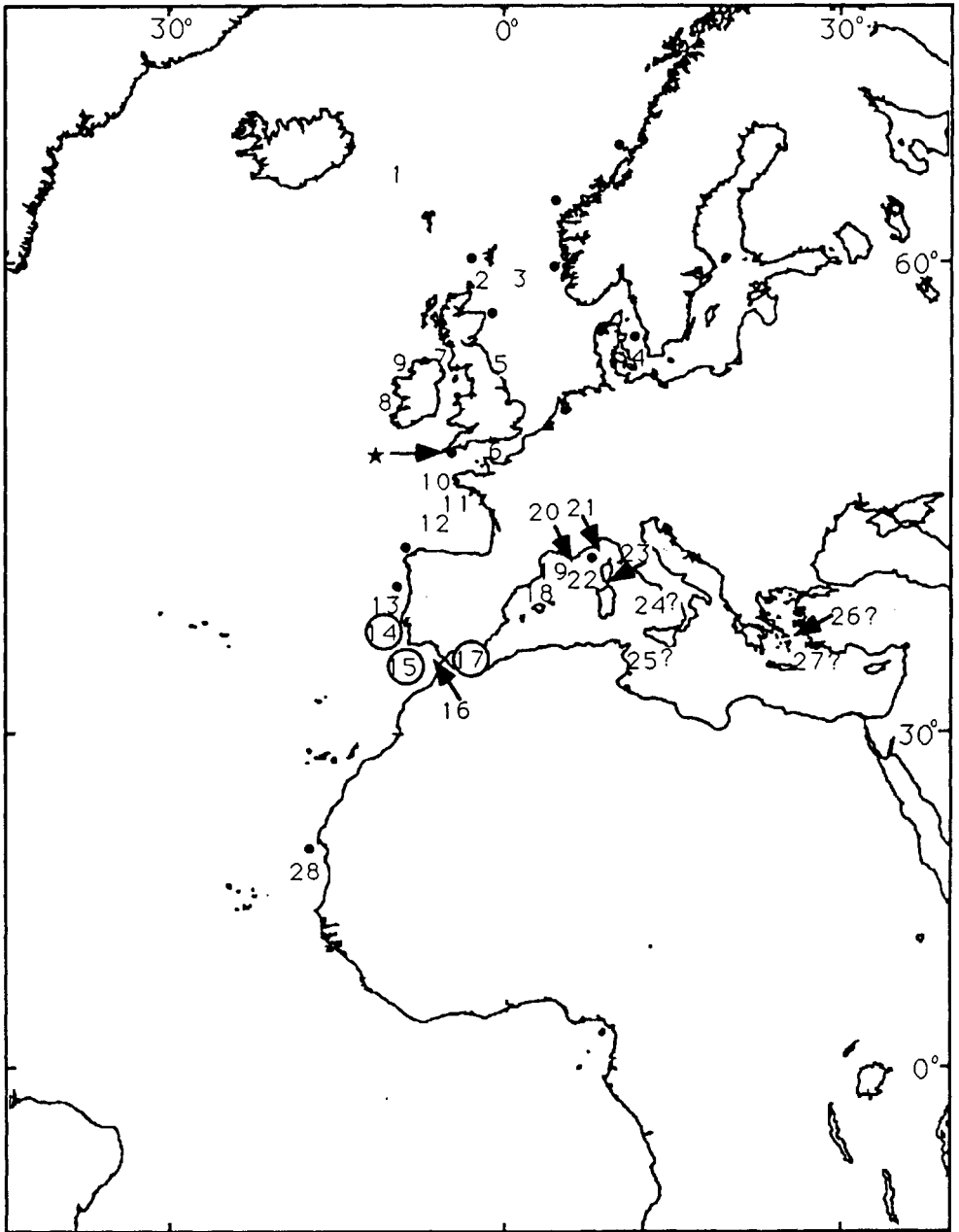


Fig. 3. Distribution of *Anapagurus laevis* (Bell, 1846). Star: type locality. Solid circles: based on present records. Numbers: based on previous records (circled numbers: material examined; numbers?: questionable material): 1-Hansen, 1908; 2-Bouvier, 1922; 3-Basford, Eleftheriou & Raffaelli, 1989; 4-Thorson, 1946; 5-Norman & Brady, 1911; 6, 11-Bouvier, 1891; 7-Henderson, 1886; 8-Tattersall, 1905; 9-Selbie, 1921; 10-Carrington & Lovett, 1882; A. Milne Edwards & Bouvier, 12-1894; 12-1899; 12, 15, 16, 20, 22, 23-1900; 13, 14-Neves, 1977; 14-Türkay, 1976; 17-García Raso, 1982; Zariquiey Alvarez, 18-1946; 19-1955; 21, 25?-Mouchet, 1931; 24?-Balss, 1926; 26?-Kocatas, 1981; Doumenc, Chintiroglou & Koukouras, 1985; 27? Lourenço, 1976; 28-Chevreux & Bouvier, 1892.

sternite of 2nd pereopods laterodistally expanded, and in males the ventromesial, distal propodal angle of 2nd pereopods with 1-3 short spines.

*Anapagurus laevis* and *A. adriaticus* spec. nov. share the overall appearance and armature, but the former species is distinguished by its much broader shield; more dilated corneae; the expanded mesial margins of the ocular acicles; the unarmed, laterodistally expanded lobes of the sternites of the 2nd pereopods; and the much larger, right sexual tube.

Remarks.— Thompson (1844) listed the names of *Pagurus laevis* and other congeners (*P. cuanensis*, *P. ulidianus*, and *P. hyndmanni*) without descriptions, figures or references to other published works, and therefore are considered nomen nudum. Bell (1846) described and illustrated *P. laevis* and the other congeners but credited authorship of these new taxa to Thompson. And for more than a century thereafter the authorship of these species was attributed to Thompson. This nomenclatorial mistake was finally corrected by Forest in 1958. Stimpson (1858) listed Bell's taxon as *Eupagurus laevis*, and subsequently Henderson (1886a) assigned it to *Anapagurus*, a newly erected subgenus of *Spiropagurus*. In 1922, Bouvier reported several pagurids collected by the "Princesse Alice II" as *A. laevis*. My examination of one of these specimens, a male collected at station 1262 (MOM 380834) reveals that it is not conspecific with *A. laevis* but rather belongs to *A. breviaculeatus*. In a preliminary report (1892) on the collections made during the campaigns of the "Hirondelle", A. Milne Edwards & Bouvier (1894) reported on several specimens they believed assignable to *A. laevis*. My reexamination of these specimens has shown that three species were confounded under this name. One specimen from station 226 is referable to *A. longispina* (the male) and one to *Pagurus pubescentulus* (A. Milne Edwards & Bouvier, 1892) (the female; new catalogue number: MOM 383821). In further studies of pagurids collected during the expeditions of the "Travailleur" and "Talisman", these authors described in 1900 the new variety *A. laevis* var. *longispina* based on a single male specimen. During my reexamination, I found that three additional males from that same station were also referable to his taxon. From the description and illustrations of *A. laevis* from the Gulf of Naples given by Fenizia (1937), it seems that he was not referring to Bell's taxon, but rather to *A. breviaculeatus* and an undescribed *Anapagurus*. Because his specimens have not been available for examination, they are questionably assigned to not *A. laevis*. Based on characters enumerated by Fenizia in his 1937 paper to distinguish *A. laevis* from *A. breviaculeatus*, Holthuis & Gottlieb (1958) questionably reported *A. laevis* from off the coast of Israel, stating that, according to their material, these two taxa could not be considered distinct species. I have examined this Israeli material and found that instead of being conspecific with Bell's taxon all specimens belong to *A. breviaculeatus* with the exception of one ovigerous female (sample 191, RMNH D 13736) and one male (sample 201, RMNH D 13728) from Haifa Bay, and one ovigerous female (sample 695, RMNH D 13744) from Atlit, which are referable to *A. longispina*, and one male from Haifa Bay (sample 191, RMNH D 13742) that belongs to *A. adriaticus* spec. nov. References to *A. laevis* from the eastern Mediterranean are found not only in the systematic literature (Lewinsohn, 1976; Balss, 1926 and 1957) but also in studies of the comparative anatomy of spermatophores (Mouchet, 1931), anthozoan systematics (Doumenc, Chintiroglou & Koukouras, 1985) and in listings (Shiber & Fattah, 1978; Kocatas, 1981). Since it is impossible to determine the identities of the specimens reported by these authors, the specimens

are questionably assigned to *A. laevis*.

Among the many specimens examined throughout the world's oceans, *A. laevis* has not been found outside the Atlantic. Therefore Bell's taxon is herein considered to be restricted to this ocean. Sarojini & Nagabhushanam (1969) reported the occurrence of *A. laevis* from the intertidal region of Lawson's Bay (India). The description and illustrations provided by these authors are insufficient to establish the identities of their specimens which were not available for examination.

In the study of the hermit crabs collected by the Belgian "Mbizi" Expedition off the African coast of Congo, Forest (1955) recorded as *A. laevis* certain specimens with more slender chelipeds and walking legs than those found in French specimens. I have had the opportunity to examine these specimens, and found that they are not conspecific with Bell's taxon, but rather belong to a new taxon, *A. congolensis* spec. nov. Furthermore, in his remarks about an ovigerous female (cited as a male in table of material examined, page 131), collected by the "Mercator" off the Island of Dassen, South Africa, Forest expressed doubt as to his identifications to *A. laevis* by listing numerous differences that he found between his material and Bell's taxon. I have examined the latter specimen and have found that it should have been assigned to *A. hendersoni*.

In the study of the pagurids collected by the "Atlantide" off the tropical western coast of Africa, Forest (1961) identified several very small but adult, specimens as *A. laevis*. He found similarities between these small, adult, tropical African specimens and juvenile *A. laevis* from temperate, northeastern Atlantic waters. The present study of these African specimens leads me to the conclusion that they are not conspecific with Bell's taxon but instead represent three different taxa, *A. wolffi* and two undescribed species, *A. vossi* spec. nov. and *A. atlantidii* spec. nov.

And finally in a study of the Decapoda Reptantia collected by the "Meteor" along the coasts of Portugal and Morocco, Türkay (1976) reported two specimens as *A. laevis*. Examination of one of them, an ovigerous female, collected at station 9c 90 (SMF 4799) has shown that it actually belongs to *A. longispina*.

*Anapagurus hyndmanni* (Bell, 1846)  
(figs. 4, 5)

*Pagurus Hyndmanni* Thompson, 1844: 182, nomen nudum (see remarks for *A. laevis*)

*Pagurus Hyndmanni* Bell, 1846: 182, 183, and unnumbered figure; White, 1850: 25 (listed); Carrington & Lovett, 1882: 390; Sinel, 1907: 216.

*Eupagurus Hyndmanni*; Stimpson, 1858: 236 (listed).

*Spiropagurus* (*Anapagurus*) *Hyndmanni*; Henderson, 1886a: 337; 1886b: 74 (by implication; see remarks for *Anapagurus*).

*Spiropagurus Hyndmanni*; Norman, 1886: 7 (listed); Scott, 1888: 258 (listed); 1897: 172.

*Anapagurus hyndmanni*; Henderson, 1888: 73 (listed); Alcock, 1905: 186 (listed); Mouchet, 1931: 80-88, 183-185, figs. 75-84, 148-150; Balss, 1944a: 464; 1944b: 599; 1956: 1439; Matthews, 1953: 265; Gordan, 1956: 302 (listed); MacDonald, Pike & Williamson, 1957: 241-243, fig. 9; Forest, 1958: 100; Pike & Williamson, 1958: 7, 8, figs. 30-33, 52; 1959: 564; Bourdon, 1960: 134, 145; Pike, 1961: 237; Pérès & Picard, 1964: 88, 115; Cardona Bendito, 1965: 144, 145, pl. II: fig. A; Zariquiey Alvarez, 1968: 259 (listed); Neves, 1977: 181, 182; García Raso, 1982: 502, fig. 2; Ingle, 1985: 764 (listed); Dauvin & Joncourt, 1989: 593.

*Anapagurus Hyndmanni*; Bouvier, 1891: 393; 1896: 152, figs. 6, 36, 37 (pictorial key); 1940: 151, figs. 105,



107C; Norman, 1905: 8 (listed); Norman & Brady, 1911: 264; Balss, 1912: 110; Selbie, 1921: 49-53, pl. VIII: figs. 4-7; Pérez, 1930: 3, figs. 4, 5; Nobre, 1931: 223, 224, figs. 123, 124; 1936: 139, pl. 44: fig. 112, pl. 46: fig. 118.

*Anapagurus curvidactylus*; A. Milne Edwards & Bouvier, 1892: 214, 215; 1900: 225 (not *Anapagurus curvidactylus* Chevreux & Bouvier, 1892); Alcock, 1905: 187 (in part); Balss, 1912: 46 (in part); De Miranda y Rivera, 1933: 30, 60 (listed); Bouvier, 1940: 149 (in part); Zariquiey Alvarez, 1968: 258 (in part).

*Eupagurus hyndmanni*; Stimpson, 1907: 216 (listed).

*Anapagurus hyndmani*; Gurney, 1942: 258: figs. 106, 107; Anadón, 1975: 206, 210, 214 (misspelling of *A. hyndmanni*).

Material.— Syntypes: 2 specimens from 2 Irish localities: off Portaferry and Belfast Bay, unknown deposition; not examined. **Northeastern Atlantic: British Isles:** 3 ♂♂ [1.9-3.6], 4 ♀♀ [2.2-2.8], Birterbuy (= Bertraghboy) Bay, Ireland, 21.xi.1891, collector A.M. Norman, ZMUC; 4 ♂♂ [3.3-3.6], 1 ♀ [2.6], Birterbuy (=Bertraghboy) Bay, Ireland, 1874?, collector A.M. Norman, USNM 6808; 5 ♂♂ [2.7-3.2], collector A.M. Norman, USNM 17007. **France:** 1 ♂ [2.4], N off Boulogne, viii.1953, collector C. Swennen, RMNH D 12520; 5 ♂♂ [2.4-5.0], 3 ovig. [2.5-2.7], off Roscoff, 25-30 m, 26.vi.1953, collector J.H. Sock, RMNH D 9916; 1 ♂ [2.7], 1 ovig. [1.9], off Roscoff, 17.ix.1958, RMNH D 12331; 10 ♂♂ [1.7-3.1], 5 ♀♀ [1.0-2.4], 2 ovig. [2.1, 2.5], off Roscoff, 16-19.ix.1958, RMNH D 12530; 1 ♀ [1.5], 2 ovig. [1.6, 2.6], off Finistère, viii; ix.1928, collector W.L. Wrede, RMNH D 3589; 1 ♂ [3.2], 2 ovig. [2.0, 2.5], Baie de Morlaix, 20.v.1958, collector W. Vervoort, RMNH D 12267; 10 ♂♂ [1.1-2.6], 3 ♀♀ [1.6-2.6], 1 ovig. [2.3], off Roscoff, bottom covered with *Zostera marina*, 29.x.1977 -26.ii.1978, collector J. Stassen, RMNH D 35233; 1 ovig. [2.6], off Roscoff, 7.viii.1952, collector H. Nouvel, RMNH D 36308; 1 ♂ [3.8], "Hirondelle" station 41, 47°19'45"N, 5°25'W, 19 m, silty bottom, 17.vii.1886, MOM 382508; 2 ♂♂ [2.6, 3.1], 2 ovig. [2.1, 2.6], Baie de Concarneau, MNHN 1827; 2 ovig. [2.1, 2.4], Baie de Concarneau, 15.ix.1958, RMNH D 12527; 3 ♂♂ [1.9-2.0], 1 ovig. [2.1], off Pointe de Moustierlin, near Quimper, 13.ix.1958, RMNH D 12529; 188 ♂♂ [1.1-3.8], 20 ♀♀ [1.8-3.6], 106 ovig. [1.8-3.6], Baie de Forest, 5-15 m, 12.ix.1958, RMNH D 12447; 1 ♂ [2.2], off îles de Glénan, 5.x.1884, collector M.J. de Guerne, USNM 22923. **Spain:** 1 ♂ [3.0], "Travailleur", along Barquero Bay, 200 m, 1882, ZMUC; 2 ♂♂ [1.7, 3.6], 1 ♀ [1.3], 1 ovig. [3.6], station 1.472, Ría de Arosa, 23.vii.1963, USNM 121788; 1 ♂ [2.2], "Josefa Camberra" station 1.579, 42°30.4'N, 08°56.2'W, Ría de Arosa, 45 m, 17.vii.1964, USNM 121789; 3 ♂♂ [1.6-1.9], 1 ♀ [1.2], 3 ovig. [1.2-1.6], "Flor da Ponte" station 1.634 (F12), 42°30.5'N, 08°56.0'W, Ría de Arosa, 18-22 m, 22.vii.1964, USNM 121790; 1 ♂ [2.9], "Flor da Ponte" station 1.681, 42°32.5'N, 08°54.0'W, Ría de Arosa, 28.vii.1964, USNM 121791; 4 ♂♂ [2.6-3.4], 1 ♀ [2.7], "Flor da Ponte" station 1.717, halfway between Lobeira de Cambados and Golfeina, Ría de Arosa, 16 m, 30.vii.1964, USNM 121792; 1 ♂ [3.1], 2 ♀♀ [1.4], Excursion RMNH station 6.1.118, Ría de Arosa, 11.8-13 m, 26.vii.1962, RMNH D 18597; 1 ♂ [1.7], Excursion RMNH station 170, Punta de la Come, Ría de Arosa, 9 m, 20.vii.1962, RMNH D 18598; 3 ♂♂ [1.5-1.7], 1 ♀ [1.5], Excursion RMNH station 1.187, near Punta del Castillo, Ría de Arosa, 11 m, 1.viii.1962, RMNH D 18599; 9 ♂♂ [2.0-3.6], 1 ♀ [2.6], 3 ovig. [2.0-3.2], Excursion RMNH station 1.155, off El Grove, Ría de Arosa, 21 m, 30.vii.1962, RMNH D 18600; 3 ♂♂ [1.6-3.4], 3 ♀♀ [1.3-1.9], Excursion RMNH station 1.189, near Centolliro, Ría de Arosa, 12 m, 1.viii.1962, RMNH D 18601; 1 ♂ [2.6], Excursion RMNH station 1.48, off Punta Cabio, Ría de Arosa, 6.5 m, 16.vii.1962, RMNH D 18602; 5 ♂♂ [2.6-3.3], Excursion RMNH station 1.429, N off Pombeiro, Península del Grove, Ría de Arosa, 15.vii.1963, RMNH D 20388; 1 ♂ [1.3], Excursion RMNH station 1.287, off Isla Palgesa, Ría de Arosa, 6.5 m, 4.vii.1963, RMNH D 20389; 4 ♂♂ [2.2-2.6], 1 ♀ [2.4], 2 ovig. [1.6, 1.8], Excursion RMNH station 1.247, off Isla Salvora, Ría de Arosa, 15 m, bottom of coarse sand, 2.vii.1963, RMNH D 20390; 1 ♂ [1.8], 1 ♀ [1.6], Excursion RMNH station 1.471, 0.5 km off Punta Porto Chunco, Península del Grove, Ría de Arosa, 27 m, 23.vii.1963, RMNH D 20391; 1 ♂ [2.7], Excursion station 1.264, 0.5 km ESE off Isla Ratas, S of Caramiñal, Ría de Arosa, 6 m, clayish bottom, 3.vii.1963, RMNH D 20392; 11 ♂♂ [1.8-3.5], 1 ♀ [1.1], 2 ovig. [2.5, 3.3], Excursion RMNH station 1.288, off San Martín, Península del Grove, Ría de Arosa, 11 m, 4.vii.1963, RMNH D 20393; 3 ♂♂ [1.1-2.1], Excursion RMNH station 1.433, off Salvores, Ría de Arosa, sandy bottom, 15.vii.1963, RMNH D 20394; 16 ♂♂ [1.9-3.8], Excursion RMNH station 1.472, 0.4 km SE off Lobeira de Cambados, S of Isla de Arosa, Ría de Arosa, 20 m, 23.vii.1963, RMNH D 20395; 1 ♂ [3.3], Excursion RMNH station 1.366, 0.2 km E off Punta de Bois, Isla Salvora, Ría de

Arosa, 8.5 m, bottom of cascajo in coarse sand, 10.vii.1963, RMNH D 20396; 1 ♂ [2.3], Excursion RMNH station 1.259, NNE off Punta Cabio, S of Caramiñal, Ría de Arosa, 19 m, 3.vii.1963, RMNH D 20397; 2 ♂♂ [1.1, 1.4], Excursion RMNH station 1.371, 0.3 km NE off Isla Salvora, Ría de Arosa, 9 m, bottom of cascajo in coarse sand, 10.vii.1963, RMNH D 20398; 1 ♂ [1.5], 1 ovig. [1.8], Excursion RMNH station 1.289, 0.8 km SSE off Punta Banquira, Isla de Arosa, Ría de Arosa, 4.vii.1963, RMNH D 20399; 1 ♂ [3.1], Excursion RMNH station 1.430, off Playa San Vicente, Península del Grove, Ría de Arosa, 15.vii.1963, RMNH D 20400; 1 ♂ [2.2], Excursion RMNH station 1.530, 0.5 km NW off Nido de Corvo, Isla de Arosa, Ría de Arosa, 5.5 m, 30.vii.1963, RMNH D 20401; 1 ♂ [1.3], 1 ovig. [1.5], Excursion RMNH station 1.344, 0.1 km N off Punta Campelo, Isla de Arosa, Ría de Arosa, 27 m, 8.vii.1963, RMNH D 20402; 1 ♂ [2.9], 1 ovig. [1.8], "Flor da Ponte" station 1.656, Ría de Arosa, 10-20 m, 24.vii.1964, RMNH D 24263; 2 ♂♂ [3.1], "Flor da Ponte" station 1.317, Ría de Arosa, 10 m, 30.vii.1964, RMNH D 24264; 6 ♂♂ [2.7-3.9], 2 ♀♀ [1.7, 1.8], Excursion RMNH station 1.472, off Lobeira de Cambados, S of Isla de Arosa, Ría de Arosa, 20 m, 23.vii.1963, RMNH D. **Portugal:** 1 ♂ [1.9], 1 ovig. [2.9], off Berlengus, 39°17'N, 9°30'W, 66 m, 2.ix.1951, collector K.W. Schuitema, RMNH D 7980; 2 ♂♂ [2.2, 2.4], off Cabo da Roca, 39°17'N, 9°30'W, 37 m, 2.ix.1951, collector K.W. Schuitema, RMNH D 7981; 1 ♂ [3.4], Excursion RMNH station 3, mouth of Río Sado, Setúbal, 5.25 m, bottom covered with algae, 29.iv.1971, RMNH D 36309; 7 ♂♂ [2.2-2.6], 2 ovig. [2.0, 2.1], Excursion RMNH, off Cabo Arnel, Ría de Faro, Faro, 29.vii.1962, RMNH D 18596. **Mediterranean Sea: Spain:** 3 ♂♂ [2.3-3.8], 3 ovig. [2.5-3.5], off Fuengirola, Málaga, 19-28 m, collector J.E. García Raso, UMDZ. One ovig. [3.3] determined as *Anapagurus laevis* and collected with 2 ♂♂ *Pagurus bernhardus*; no data available; USNM 63400.

**Diagnosis.**— Shield approximately as long as broad. Rostrum slightly exceeded by lateral projections. Lateral projections with short to moderately long, submarginal spine.

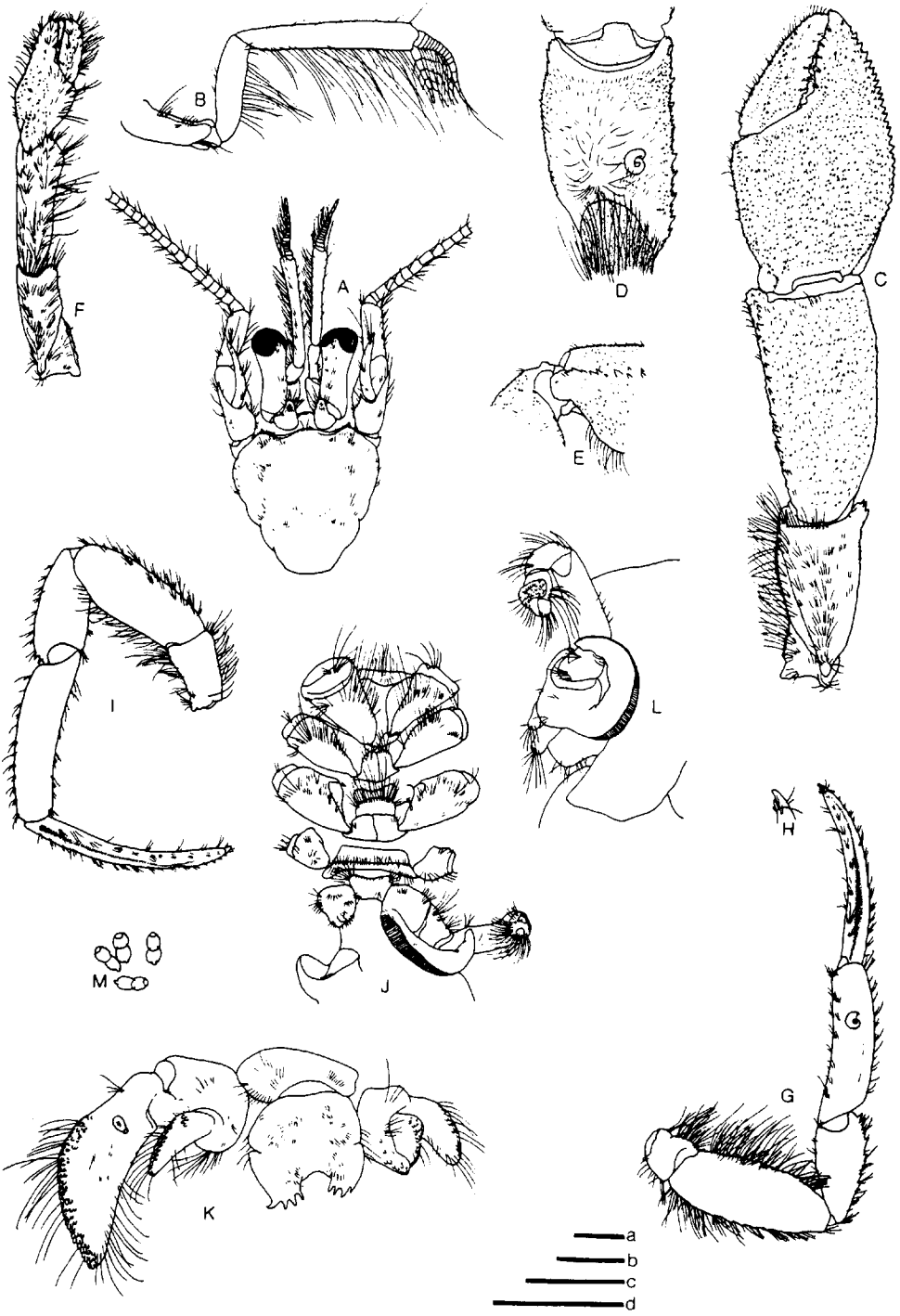
Ocular peduncles approximately  $\frac{3}{5}$  length of shield, with corneae slightly dilated. Ocular acicles narrowly triangular, with long, distal, submarginal spine. Interocular plate unarmed.

Antennular peduncles exceeding distal margin of corneae by  $\frac{1}{2}$  or more than  $\frac{1}{2}$  length of penultimate segment. Ultimate antennular segment about twice as long as penultimate segment, with dorsolateral and dorsomesial rows of short setae, and moderately long, dorsolateral, distal seta; ventral margins of ultimate and penultimate segments, each with row of tufts of very long setae that exceed length of ventral antennular flagellum; basal segment with lateromedial spine.

Antennal peduncles overreaching distal margin of corneae by approximately  $\frac{1}{2}$  length of ultimate segment. Antennal acicles terminating in short spine, approximately reaching distal margin of corneae.

Chela of right cheliped broad (females) or moderately broad (males). Fingers curved ventrally, strongly so in mature males. Dactyl subequal to length of palm, triangular in cross section, with strong, dorsomedial and ventromesial, spinulose ridges; all surfaces with small spinules; ventral surface with tufts of long setae. Palm

Fig. 4. *Anapagurus hyndmanni* (Bell, 1846). A-L: ♂ (SL = 3.3 mm). Excursion RMNH station 1.366, off Isla Salvora, Ría de Arosa, Spain, RMNH D 20396: A, shield and cephalic appendages; B, left antennule (lateral view); C, right cheliped (dorsal view); D, carpus of same (ventral view) with a serpulid polychaete tube; E, joint of palm and carpus of same (mesial view); F, left cheliped (dorsal view); G, right 2nd pereopod (mesial view) with a serpulid polychaete tube on propodus; H, tip of dactyl of same; I, right 3rd pereopod (mesial view); J, sternum; K, extremity of abdomen, uropods and telson (folliculinid type 1 on exopod of left uropod); L, left sexual tube (lateral view). M, folliculinid type 2 on abdomen of ♂ (SL = 2.9 mm), "Flor da Ponte" station 1.681, 42°32.5'N, 08°54.0'W, Ría de Arosa, Spain, USNM 121791. Scales equal 1.0 mm: a: A, C-G, I, J; b: L; c: B, H, K; d: M.



approximately  $\frac{2}{3}$  length of carpus, dorsomesial margin with spinulose ridge on proximal half; dorsal surface somewhat convex, with numerous spinules and scattered, short setae, without ridge near dorsomesial margin proximally; dorsolateral margin with row of spinules increasing in size distally but becoming obsolete near claw; dorsoproximal margin with well-developed lobes, laterally and mesially, larger mesial lobe with concavity to fit the dorsomesial, distal lobe of carpus when chela is flexed; ventroproximal margin with skewed, subquadrate sinus near ventromesial margin. Carpus exceeding merus by approximately  $\frac{1}{3}$  own length, shorter in females; dorsomesial margin with irregular row of closely spaced, short spines; dorsomesial, distal angle produced into spinulose subcircular structure; dorsodistal margin with very weak, subcircular projections adjacent to dorsomesial and dorsolateral, distal angles; mesial face somewhat depressed; dorsolateral face rounded, slightly inflated, without delimiting, dorsolateral margin; dorsolateral, distal angle produced into small subcircular, spinulose lobe; ventromesial margin subcircular in mesial view; moderately long, ventral length between shallow, subcircular, ventrodistal and ventroproximal margins; mesial and dorsolateral faces each with spinules and scattered, short setae; ventral surface with spinules and scattered setae, short in females, very long on proximal half in males. Dorsal margin of merus with row of moderately long setae and moderately long, distal spine; ventromesial margin with short distal spine and slightly developed protuberance (males); ventrolateral margin with 4 or 5 strong spines; ventral surface with spinules and scattered setae, short in females, very long in males. Ischium with 1 spinule on ventrolateral margin partly covered by tufts of setae, short in females, long in males; ventromesial margins serrate. Coxae of chelipeds with 1 short, ventrolateral, distal spine.

Dactyl of left cheliped with median row of spinules on dorsal surface; all surfaces with numerous tufts of moderately long setae. Dorsomesial and dorsolateral margins of carpus, each with 2 or 3 strong, widely spaced spines on distal half.

Ambulatory legs with dactyls exceeding propodi by  $\frac{1}{5}$  to  $\frac{1}{4}$  own length, lateral and mesial faces each with row of closely spaced tufts of short, stiff setae near dorsal and ventral margins, and with longitudinal sulcus, broad (2nd) or narrow (3rd). Propodi exceeding carpi by nearly  $\frac{1}{3}$  own length; dorsal surfaces each with row of closely spaced tufts of short, stiff setae, with short spinules (2nd) or unarmed (3rd); lateral and mesial faces each with row of widely spaced, stiff, short setae near dorsal and ventral margins; ventromesial distal angle unarmed but with tuft of stiff, short setae. Carpi approximately  $\frac{2}{3}$  length of meri; dorsal surfaces with row of tufts of short, stiff setae and short spines (2nd) or 1 or 2 short spinules on proximal half and 2 or 3 short distal spines (3rd). Dorsal surfaces of meri serrate (2nd) or unarmed (3rd), each with row of tufts of moderately long setae; ventral margins with row of spinules (2nd) or unarmed (3rd), each with row of moderately long setae. Lobes of sternite of 2nd pereopods unarmed, distally rounded. Anterior lobe of sternite of 3rd pereopods subrectangular; anterior margin with tufts of moderately long setae. Males with moderately long, left sexual tube, recurved to level of coxa of 5th right pereopod; coxa of right 5th pereopod with short, curved sexual tube backwardly directed, partly covered by tufts of moderately long setae; three uniramous pleopods. Distal, protopodal lobe of right uropod equaling length of endopod, giving appearance of a chelate structure.

Telson with asymmetrical, posterior lobes separated by wide, shallow cleft; terminal margins each with 4 short spines; lateral margins unarmed but with tufts of moderately long setae.

Colour.— The colour of *Anapagurus hyndmanni* is pale, dull red and its ova are green. (Carrington & Lovett, 1882). The cornea is deeply pigmented (Selbie, 1921).

Most specimens of the present preserved (ethanol) collections have the chelipeds and ambulatory legs with blotches of orange, and the antennal flagella with bands (2 to 4 articles long) of deep orange, occasionally red.

Related organisms.— The following gastropod shells occupied by *A. hyndmanni* have been recorded: *Turritella terebra* by Bell (1846), *Turritella* sp. by Carrington & Lovett (1882), *Littorina* sp. by Sinel (1907), and *Nassarius* sp. (= *Hinia* sp.) by Neves (1977). In the present collections the following shells occupied by *A. hyndmanni* have been found: *Hinia reticulata* (Linnaeus, 1758) (8 specimens: RMNH D 7980, RMNH D 9916, RMNH D 25233, USNM 12170, and ZMUC- 21.xi.1891); *Gibbula pennanti* (Philippi, 1836) (5 specimens: RMNH D 24262, RMNH D 35233, and USNM 121791); *Gibbula albida* Gmelin (1 specimen, ZMUC-21.xi.1891); *Ocinebrina aciculata* (Lamarck, 1822) (2 specimens, RMNH D 35233); *Turritella biplicata* (1 specimen, USNM 121788); and unidentified shell (RMNH D 35233). In the present collections the following organisms were found on shells occupied by *A. hyndmanni*: Bryozoa: on *Turritella biplicata* (USNM 121788); on *Gibbula albida* and *Hinia reticulata* (ZMUC- 21.xi.1891). Protozoan folliculinid type 1 (see below) outside one shell of *Hinia reticulata* and inside two shells of *Ocinebrina aciculata* and one of *Gibbula pennanti* (RMNH D 35233). Annelida: Polychaeta: Serpulidae: outside and/or inside two shells of *Gibbula pennanti*, and outside two shells of *Ocinebrina aciculata* and one shell of *Hinia reticulata* (RMNH D 35233); and outside the shell of *Gibbula albida* (ZMUC- 21.xi.1891); and Terebellidae: RMNH D 35233 (near apex of unidentified shell (RMNH D 35233).

*Anapagurus hyndmanni* has been reported as a host for the following parasites: nematomorph *Nectonema agile* Verrill and turbellarian *Fecampia erythrocephala* by Mouchet (1931); isopod *Athelges tenuicaudis* by Bourdon (1960) and Pike (1961); and rhizocephalan *Peltogasterella sulcata* (as *Gemmosaccus sulcatus*) by Bourdon (1960). The ciliated protozoan *Folliculina* (= *Pebrilla*) *paguri* (Giard, 1888) reported by Balss (1956) on *A. hyndmanni* is the only recorded folliculinid in the genus *Anapagurus*. In the present collections, 57 specimens of *A. hyndmanni* were hosts of two species of folliculinids, herein referred to as type 1 (fig. 4K), with ovate test, and type 2 (fig. 4M) with a medial transverse constriction and a small, apical knob. The folliculinids usually ranged in number from 1 to 15 (occasionally 24 or 26) specimens per host; most tests were cemented to the posterior abdomen, telson, uropods, and occasionally to the shield. Hosts usually have either one of the two species of folliculinids, however both taxa were found in three specimens of *A. hyndmanni* (RMNH D 9916 and RMNH D 20395). Folliculinids type 1 were found in 14 specimens of *A. hyndmanni* (RMNH D 9916, 12447, 12530, 18597, 18598, 18599, 20390, 24263 and 35233). Folliculinids type 2 were associated with 40 specimens of *A. hyndmanni* (RMNH D 1827, 12267, 12331, 12447, 12530, 18597, 18600, 18601, 20388, 20393, 20395 and 24264; Excursion RMNH station 1.472; and USNM 121791).

One, occasionally two tubes of serpulid polychaetes were attached commonly to the carpus of the right cheliped ventrally or dorsally, occasionally to the propodus of

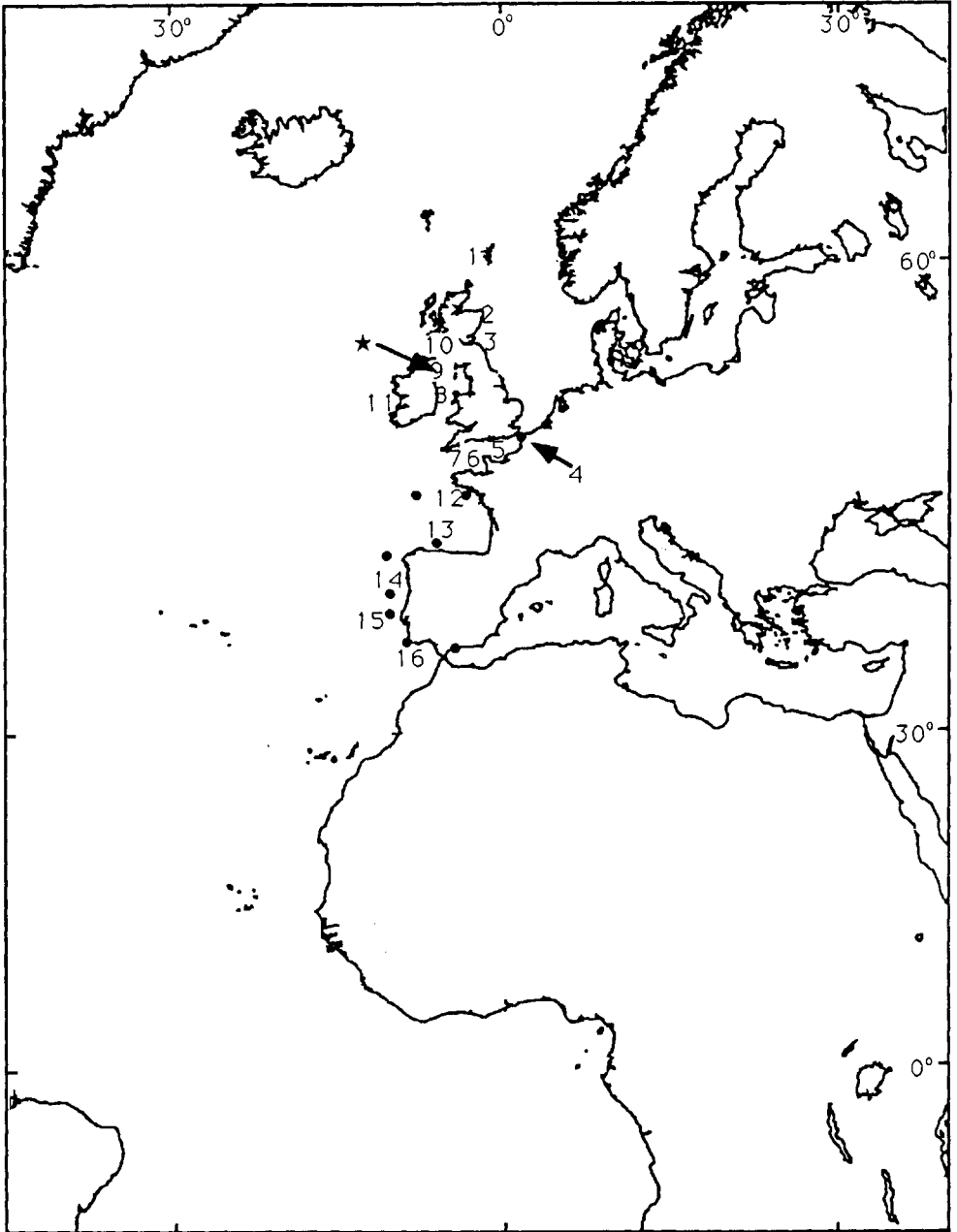


Fig. 5. Distribution of *Anapagurus hyndmanni* (Bell, 1846). Star: type locality. Solid circles: based on present records. Numbers: based on previous records: 1, 3, 6, 7, 8, 11-Carrington & Lovett, 1882; 2-Balss, 1926; 3-Norman & Brady, 1911; 4, 5, 12-Bouvier, 1891; 10-Henderson, 1886; 13-A. Milne Edwards & Bouvier, 1892, 1900 (material examined); 14-Cardona Bendito, 1965; 15, 16-Nobre, 1931, 1936.

the right 2nd pereopod mesially (RMNH D 12447, 18597, 20395 and 20396).

Filamentous green algae (Chlorophyta) were found attached to the carpus of the left cheliped dorsally, the merus of the ambulatory legs, and the antennal acicles and flagella (RMNH D 12447, 20388 and 20390).

Distribution.— Northeastern Atlantic: from the Shetland Islands (Carrington & Lovett, 1882) to Costa do Algarve (southern Portugal). Mediterranean Sea: off Fuen-girola, Málaga (southern Spain). Depth range: 0 to 200 m; most frequently found in depths of 5 to 30 m.

Affinities.— In the general similarity of chelipeds (e.g., coxae with ventrolateral distal spines; the right chelae of males with ventrally curved fingers and heavily setose carpus, merus, and ischium ventrally) and in the unarmed, ventromesial, distal angle of propodi of 2nd pereopods, *A. hyndmanni* appears close to *A. curvidactylus*. *Anapagurus hyndmanni* may be distinguished from the latter by its much longer, ultimate antennular segment bearing ventral setae longer than ventral antennular flagellum, longer antennal acicles, the presence of longitudinal sulci on the lateral and mesial faces of the ambulatory legs, and the much shorter left sexual tube.

Remarks.— A. Milne Edwards & Bouvier (1892) assigned a relatively large specimen (SL= 3.0 mm) collected by the "Travailleur" off Barquero in northern Spain at a depth of 200 m, to *A. curvidactylus*. In 1900, these authors remarked that the specimen had certain differences (i.e., larger right chela, dactyls of ambulatory legs with longitudinal sulci) from the typical Chevreux & Bouvier's taxon; they attributed these differences to the age of the specimen. I have been able to compare this specimen with the extensive collection at Leiden from Ría de Arosa (northwest Spain) assigned to *A. hyndmanni*, and believe the A. Milne Edwards & Bouvier's specimen is conspecific with Bell's taxon. The Alcock (1905), Balss (1921), Bouvier (1940), and Zariquiey Alvarez's (1968) references are to *A. curvidactylus* and include the above specimen of *A. hyndmanni* from Barquero.

In the study of the decapod and stomatopod crustaceans of Portugal, Nobre illustrated *Anapagurus Hyndmanni* with a photograph (fig. 123, 1931 edition; pl. 44: fig. 112, 1936 edition) that was probably reversed in printing so that the actual right cheliped appeared as the left.

*Anapagurus chiroacanthus* (Lilljeborg, 1856)  
(figs. 6, 7)

*Pagurus chiroacanthus* Lilljeborg, 1856: 118 [type locality: off Kullaberg, Scania (=Skåne), southwest Sweden]; Henderson, 1886b: 75.

*Pagurus ferrugineus* Norman, 1861: 273, 274, pl. XIII: figs. 1-3.

*Pagurus chiroacantha*; Sars, 1872: 256 (misspelling of *P. chiroacanthus*).

*Spiropagurus (Anapagurus) ferrugineus*; Henderson, 1886a: 338, 1886b: 75 (by implication; see remarks for *Anapagurus*).

*Spiropagurus (Anapagurus) chiroacanthus*; Henderson, 1886a: 353; Gurney, 1942: 153.

*Anapagurus chiroacanthus*; Henderson, 1888: 73 (listed); Bouvier, 1896: 153, figs. 40 and 41; Norman, 1905: 8 (listed); Lagerberg 1908: 61, pl. I: fig. 10; Norman & Brady, 1911: 264; Elmhirst, 1912: 23; Selbie, 1921: 48; Balss, 1926: 375, 377, 379; 1956: 1433, 1459, 1466; Nilsson-Cantell, 1926: 2-11; Fenizia, 1937: 29-31, fig. 20; Bouvier, 1940: 148, fig. 102; Gurney, 1942: 261; Reinhard, 1942: 412; Thorson, 1946: 339, 340; Zariquiey Alvarez, 1946: 122, 123 (listed); 1955: 402; 1968: 257, 258; Buddenbrock, 1948: 1034, 1037; Pike, 1953: 29, 233; 1961: 226, 236, 237; Forest, 1955: 44, 127, 128, pl. 6, fig. 1; 1958:

100; 1961: 240, figs. 6, 10, 14, 17; 1965: 355; Gordan, 1956: 302 (listed); MacDonald, Pike & Williamson, 1957: 243-246, fig. 10; Füller, 1958: 173; Pike & Williamson, 1958: 7, 8, figs. 34-38, 53; 1959: 564; 1960: 525; Bourdon, 1968: 195; Hazlett, 1968a: 138; 1968b: 246, 247, 249; 1981: 8; Samuelsen, 1970: 44; Naylor, 1972: 70; Neves, 1977: 180, 181, fig. 9C; Stachowitsch, 1980: 74, 93; Calafiore, 1981: 20, 25, 26; Kocatas, 1981: 162; Schembri, 1982: 872; Crothers & Crothers, 1983: 763, 783; Salmon, 1983: 148; Ingle, 1985: 764 (listed); 1990: 105-134; Høeg & Lützen, 1985: 32, 39; Markham, 1986: 154.

*Pagurus chiroacanthus*; Aurivillius, 1891: 33, pl.V: fig. 5 (misspelling of *P. chiroacanthus*).

*Anapagurus brevicarpus* A. Milne Edwards & Bouvier, 1892: 215; 1898: 1247 (listed); 1899: 67; 1900: 223, pl.XXV: figs. 23-26, pl. XXVIII: fig. 11; Bouvier, 1896: 153, figs. 38, 39 (pictorial key); 1922: 31; 1940: 150, 151, figs. 104, 107 D (listed); Monod, 1932: 487 (listed); De Miranda y Rivera, 1933: 30, 60 (listed); Forest, 1958: 100 (listed); Zariquiey Alvarez, 1968: 258, 259 (listed); Ingle, 1985: 764 (listed).

*Eupagurus chiroacanthus*; Norman, 1886: 7; Sars, 1899: 213; Stimpson, 1907: 215 (listed).

*Spiropagurus chiroacanthus*; Sars, 1890: 155, pl. iii; 1899: 267, pl. 89: fig. X; Bouvier, 1891: 68, 75; Gurney, 1939: 98 (listed).

*Anapagurus chiroacanthus*; Balss, 1924: 783 (misspelling of *A. chiroacanthus*).

? *Anapagurus brevicarpus*; Mouchet, 1931: 9092, fig. 87; Forest, 1961: 243; Cardona Bendito, 1965: 146.

*Anapagurus chiroacanthus* var. *gracilis* Fenizia, 1937: 31, 32, fig. 21; Pike & Williamson, 1959: 564.

*Anapagurus chiroacanthus* var. *cristatus* Fenizia, 1937: 32, 33, fig. 22.

Material.— Syntypes, BMNH; not examined. **Northeastern Atlantic: Norway:** 1 ♂ [1.9], 2 ♀♀ [2.0, 2.1], "Eugenie Expedition" station N: R21, off Farsund, NHRM 1437; 1 ♂ [2.9], "Ing. O. Gladans Expedition", off Christiansand, 91 m, shelly bottom, 1871, collector Lindahl, NHRM 1504; 4 ♂♂ [1.6-2.4], 1 ♀ [2.2], Leerrviksfjord, 128 m, shelly bottom, vii.1880, collector C. Bovallius, NHRM 2469; 2 ♂♂ [1.8, 1.9], off Haugesund, 43.9 m, sandy bottom, vii.1880, collector C. Bovallius, NHRM 2478; 2 ♂♂ [1.4, 2.1], 2 ovig. [1.9], off Haugesund, 73 m, shelly bottom, v.viii.1880, collector C. Bovallius, NHRM 3486; 2 ♂♂ [1.5], 1 ovig. [2.1], off Norwegian coast, collector A. M. Norman, USNM 17008; 1 ♂ [2.8], Skagerak, collector Malm, ZMB 18603; 1 ♂ [1.8], 60°33'N, 4°50'E, 12-20 m, bottom of shell, gravel and *Laminaria*, 1.ix.1981, RMNH D; 1 ♂ [2.3], 60°36'N, 4°55'E, 30-50 m, sandy bottom, 4.ix.1981, RMNH D; 3 ♂♂ [0.9-2.2], 1 ♀ [0.9], 3 ovig. [0.9], 1 intersex [1.2], 60°15'N, 5°13.5'E, 10-16 m, 11.ix.1961, RMNH D 19128; 9 ♂♂ [1.0-2.1], 2 ♀♀ [1.2, 5.6], 5 ovig. [1.2-2.4], 60°11'N, 5°2'E, 23-35 m, 6.ix.1961, RMNH D 19129; 1 ♂ [2.6], 1 ovig. [2.2], 63°39'N, 9°30'E, 5-10 m, 31.viii.1961, RMNH D 19130; 1 ovig. [1.6], 63°40'N, 9°14'E, 200 m, 29.viii.1961, RMNH D 19132; 2 ♂♂ [2.0], 2 ♀♀ [1.4, 1.5], 1 ovig. [0.8], off S Bergen, ca 1 m, 7.ix.1961, RMNH D 19133; 4 ♂♂ [2.0-2.9], 2 ♀♀ [1.0, 1.8], 3 ovig. [2.5-2.7], 60°15.5'N, 5°11'E, 30-35 m, 9.ix.1961, RMNH D 19426; 3 ♂♂ [2.1-2.3], 63°37'N, 9°27'E, 30 m, 31.viii.1961, RMNH D 19427; 2 ♂♂ [1.5, 2.8], 59°15.5'N, 5°11.5'E, 18 m, 9.ix.1961, RMNH D 19429; 2 ♂♂ [1.4, 2.0], 63°43'N, 9°48'E, 7-50 m, 28.viii.1961, RMNH D 19432; 1 ♂ [2.3], 63°36'N, 9°27'E, 10-25 m, 22.viii.1963, RMNH D 20218; 2 ♂♂ [1.9, 2.3], 1 ♀ [2.0], 1 ovig. [1.9], 63°39'N, 9°49'E, 200 m, 27.viii.1965, RMNH D 21858; 2 ♂♂ [2.0, 2.3], 63°38'N, 9°18'E, 30 m, 26.viii.1965, RMNH D 24169; 1 ♂ [2.7], 63°42'N, 9°27'E, 20-70 m, sandy bottom, 26.viii.1965, RMNH D 24170; 3 ♂♂ [1.5-2.7], 1 ♀ [1.2], 63°41'N, 9°42'E, 25-50 m, sandy bottom, 31.viii.1965, RMNH D 24172; 1 ♀ [2.4], 63°41'N, 9°41'E, 15-20 m, bottom of *Laminaria*, 22.viii.1967, RMNH D 24173; **Sweden:** 7 ♂♂ [2.0-3.0], 6 ♀♀ [1.3-2.4], 4 ovig. [1.9-2.8], 3 intersex [2.2-7.5], off Sorriga, Gullmarn, Bohuslän, bottom of shells and sponges, collector S. Lovén, NHRM 1020; 2 ♂♂ [2.5, 2.7], 3 ♀♀ [1.9-2.5], 9 ovig. [1.5-3.2], off Sorriga, Gullmarn, Bohuslän, bottom of shells and sponges, collector S. Lovén, NHRM 1021; 6 ♂♂ [1.8-2.9], 12 ♀♀ [2.0-2.7], 28 ovig. [1.9-3.0], off Sorriga, Gullmarn, Bohuslän, bottom of shells and sponges, collector S. Lovén, NHRM 1022; 1 ♂ [2.7], off Sorriga, Bohuslän, NHRM 1041; 2 ♂♂ [2.8, 2.9], 2 ovig. [2.6], off Gullmarn, Bohuslän, NHRM 1171; 1 ovig. [1.8], off Stavanger, collector V. Friesen, NHRM 1182; 5 ♂♂ [1.1-1.5], off Sorriga, Bohuslän, NHRM 1407; 1 ♂ [1.8], off Gullmarn, Bohuslän, shallow depth, bottom of algae, NHRM 1411; 1 ♂ [1.8], off Bokevik, Bohuslän, 12.8 m, NHRM 1412; 10 ♂♂ [1.2-2.0], 5 ♀♀ [1.5-1.8], 7 ovig. [1.4-1.9], 1 mile off Koster, 36.6 m, rocky bottom, vii.1865, NHRM 1414; 1 ♂ [1.3], 3/4 mile off Nord Koster, Bohuslän, 36.6 m, sandy bottom, 1865, NHRM 1418; 2 ♂♂ [1.0, 1.8], off Kosterfjorden, Bohuslän, 27.4-36.6 m, sandy bottom, 1865, collector Ljungman, NHRM 1424; 16 ♂♂ [1.4-2.4], 8 ♀♀ [1.3-1.5], 8 ovig. [1.2-2.0], off Kosterfjorden, Bohuslän, 9.1-27.4 m, rocky bottom, 1865, collector Ljungman, NHRM



1425; 13 ♂♂ [1.4-2.5], 2 ♀♀ [1.6, 1.9], 6 ovig. [1.1-1.8], off Kosterfjorden, Bohuslän, 27.4-36.6 m, sandy bottom, 1865, collector Ljungman, NHRM 1427; 5 ♂♂ [1.2-1.9], 2 ♀♀ [1.3], 3 ovig. [1.5-1.8], 5 intersex [1.0-1.6], off Kosterfjorden, Bohuslän, 9.1-27.4 m, rocky bottom, 1865, collector Ljungman, NHRM 1428; 8 ♂♂ [1.8-2.6], 8 ♀♀ [1.5-2.2], 5 ovig. [1.7-2.0], 1 intersex [1.8], off Stora Väderön, Bohuslän, 45.7m, 1869, collector Olsson, NHRM 1429; 5 ♂♂ [1.0-2.7], 5 ♀♀ [1.5-2.7], 3 ovig. [1.5-2.6] off Lindö, Bohuslän, 54.9 m, 1869, collector Olsson, NHRM 1433; 1 ovig. [2.0], off Styrsö ranna, Bohuslän, 54.9 m, 1869, collector Olsson, NHRM 1435; 1 ♂ [2.0], 1 ovig. [1.9], 54.9 m, 1869, collector Olsson, NHRM 1436; 2 ♂♂ [1.6, 1.9], off St. Väderön, Bohuslän, 100.6 m, vi.1869, collector Olsson, NHRM 1505; 2 ♂♂ [1.9, 2.1], off Väderöarna, Bohuslän, 27.4-54.9 m, sandy bottom, collectors C. Bovallius & Théel, NHRM 1529; 7 ♂♂ [1.1-2.1], 2 ♀♀ [1.0, 1.2], 3 ovig. [1.4-1.8], off Väderöarna, Bohuslän, 54.9 m, sandy bottom, vii.1877, collectors C. Bovallius & Théel, NHRM 1530; 7 ♂♂ [0.9-2.0], 10 ♀♀ [0.9-1.5], 3 ovig. [1.2-1.4], 1 intersex [2.2], off Väderöarna, 54.9 m, sandy bottom, vii.1877, collectors C. Bovallius & Théel, NHRM 1531; 5 ♂♂ [1.8-2.4], 1 ♀ [2.1], 1 ovig. [1.6], off Väderöarna, Bohuslän, 54.9 m, sandy bottom, 12.vii.1877, collectors C. Bovallius & Théel, NHRM 1532; 1 ovig. [1.4], off Väderöarna, Bohuslän, 109.7 m, bottom of corals, vii.1877, collectors C. Bovallius & Théel, NHRM 1537; 1 ovig. [2.3], "Gunhild" station 75, Väderöarna, Bohuslän, 73.2-91.4 m, bottom of corals, 28.vii.1877, collectors C. Bovallius & Théel, NHRM 1538; 2 ♂♂ [1.6, 1.9], off Kilsund, Bohuslän, 91.4 m, shelly bottom, vii.1877, collectors C. Bovallius & Théel, NHRM 1542; 1 ♂ [2.7], off Lysekil, Bohuslän, 45.7 m, vii.1877, collectors C. Bovallius & Théel, NHRM 1545; 2 ♀♀ [1.7], 2 ovig. [1.9, 2.0], off Kosterfjorden, Bohuslän, 21.9-32.9 m, rocky bottom, viii.1865, collector Ljungman, NHRM 1872; 1 ♀ [2.9], "Gunhild" station unknown, off Utanför, Helsingborg, 32.9-40.2 m, bottom of sand and clay, 17.vii.1878, collectors Théel & Trybom, NHRM 2250; 1 ♀ [2.1], 1 ovig. [2.2], off Väderöarna, Bohuslän, 5.viii.1879, NHRM 2342; 2 ♂♂ [1.8, 2.1], 1 ♀ [2.1], off Väderöarna, Bohuslän, 1877, NHRM 2352; 9 ♂♂ [1.4-2.5], 1 ♀ [1.4], 1 ovig. [1.4], off Väderöarna, Bohuslän, viii.1881, NHRM 2539; 1 ♀ [2.9], 3 ovig. [2.4-2.9], 1 intersex [2.0], off Gullmarn, Bohuslän, viii.1881, collector Svedérus, NHRM 2549; 4 ♂♂ [2.0-2.7], 1 ovig. [1.9], off Väderöarna, Bohuslän, viii.1882, collector Aurivillius, NHRM 2642; 1 ♀ [2.0], off Hallö, Bohuslän, 36.6 m, 1884, NHRM 2758; 1 ♂ [2.7], 1 ovig. [3.0], off Kristinebergs Zoological Station, Bohuslän, 1885, NHRM 2821; 1 ♂ [2.0], off Gullmarn, Strumpeskagen, Bohuslän, 17.vii.1876, collector C. Bovallius, NHRM 3152; 1 ♂ [1.5], off Gullmarn, Strumpeskagen, Bohuslän, 91.4 m, 5.vii.1876, collector C. Bovallius, NHRM 3221; 3 ovig. [2.1-2.6], off Flatholmen, Bohuslän, 54.9 m, 8.vii.1876, collector C. Bovallius, NHRM 3223; 4 ♂♂ [1.2-2.5], 3 ♀♀ [1.7-2.2], 3 ovig. [1.8-2.1], off Nord Koster, Bohuslän, 1869, collector C. Bovallius, NHRM 3224; 1 ♂ [2.5], 1 ovig. [2.5], off Stångehufvud, Lysekil, Bohuslän, 19.vii.1876, NHRM 3225; 1 ♂ [2.1], 1 ovig. [1.9], off Stångehufvud, Lysekil, Bohuslän, 19.vii.1876, NHRM 3226; 2 ♂♂ [2.1, 2.9], 1 ovig. [1.8], off Stångehufvud, Lysekil, Bohuslän, 19.vii.1876, NHRM 3227; 1 ♂ [2.8], 1 ♀ [2.9], 1 intersex [2.2], off Ullholmsrännan, Bohuslän, 31.v.1890, collector C. Aurivillius, NHRM 3484; 1 ovig. [2.7], off Harpöbrott, Bohuslän, v.1890, collector C. Aurivillius, NHRM 3485; 2 ♂♂ [2.7, 2.9], off Gullmarn, Flatholmsrännan, 17.vii.1890, collector C. Aurivillius, NHRM 3519; 2 ♂♂ [2.2, 2.6], 5 ovig. [2.0-2.7], off Kristineberg Zoological Station, Bohuslän, 1893, NHRM 3682; 4 ♂♂ [1.6-2.6], off Kosterfjorden, Kostersten, Bohuslän, 109.7-182.9 m, 3.vii.1895, collector C. Aurivillius, NHRM 3685; 1 ♂ [2.0], 1 ♀ [2.3], 1 ovig. [1.7], off Väderöarna, Bohuslän, bottom of clay, 29.vii.1896, collector I. Arvidsson, NHRM 3686; 2 ♀♀ [1.7, 2.4], 2 ovig. [1.9, 2.1], off Kummelbanken, 1900, collector T. Tullberg, NHRM 4173; 1 ♂ [2.4], off Kummelbanken, 1900, collector T. Tullberg, NHRM 4186; 4 ♂♂ [1.8-3.0], 1 ♀ [2.8], 4 ovig. [2.5-2.7], 1 intersex [1.9], north off Flatholmen, Gullmaren, 80 m, 1.vii.1906, collector T. Lagerberg, NHRM 4255; 2 ovig. [2.4, 2.5], off Gåsöräna, 40 m, 27.vi.1906, collector T. Lagerberg, NHRM 4256; 3 ♂♂ [2.2-2.5], 1 ♀ [1.5], 3 ovig. [1.8-3.1], 1 intersex [2.1], off Svartskär-Vinga, 26 m, 31.vii.1906, collector T. Lagerberg, NHRM 4261; 12 ♂♂ [1.8-3.0], 24 ovig. [1.8-2.7], off Gullmaren, vii.1923, collector C.A. Nilsson-Cantell, NHRM 4676; 64 ♂♂ [1.6-3.0], 5 ♀♀ [1.4-2.7], 28 ovig. [1.5-3.1], 1 intersex [1.9], off Gåsöräna, Gullmaren, vii.1923, collector C.A. Nilsson-Cantell, NHRM 4677; 26 ♂♂ [1.6-3.0], 2 ♀♀ [2.1, 2.9], 21 ovig. [1.7-2.0], 2 intersex [2.1, 2.6], off Smedjebrotten, Bohuslän, 16.vi.1923, collector C.A. Nilsson-Cantell, NHRM 4678; 1 ♀ [1.5], off Bovallstrand, Lygnösundet, Bohuslän, 12 m, sandy bottom, 23.vii.1935, collector S. Bock, NHRM 5174; 1 ovig. [2.8], off Kristineberg, 1905, collector Y. Schwartz, NHRM 5772; 1 ♂ [2.7], off west coast, MCZ 12688; 1 ♂ [2.0], 1 ovig. [1.8], 58°12'N, 11°20'E, 20-35 m, sandy bottom, 9.ix.1981, RMNH D; 3 ♂♂ [1.5-2.7], 58°16'N, 11°25'E, 35

m, bottom of gravel, 10.ix.1981, RMNH D; 14 ♂♂ [1.8-2.8], 20 ♀♀ [1.4-2.6], 2 ovig. [2.1, 2.2], 3 intersex [1.4-2.1], 58°16'N, 11°25'E, 30 m, 16.ix.1961, RMNH D 19131; 7 ♂♂ [1.4-2.3], 58°13.5'N, 11°25'E, 30-40 m, 16.ix.1961, RMNH D 19425; 3 ♂♂ [2.4-2.8], 58°14.5'N, 11°30.5'E, 7 m, 15.ix.1961, RMNH D 19428; 15 ♂♂ [1.5-2.9], 18 ♀♀ [1.6-2.7], 2 ovig. [2.5], 1 intersex [2.0], 58°15.5'N, 11°25.5'E, 25 m, 16.ix.1961, RMNH D 19431; 5 ♂♂ [2.1-2.8], 2 ♀♀ [2.0, 2.1], 1 intersex [2.0], 58°14'N, 11°25'E, 33-40 m, 16.ix.1961, RMNH D 19433; 2 ♂♂ [1.8], 58°12.5'N, 11°19'E, 35 m, 19.ix.1961, RMNH D 19434; 14 ♂♂ [1.6-2.7], 3 ♀♀ [1.9-2.1], 1 ovig. [2.0], 58°16'N, 11°25'E, 25 m, 29.viii.1961, RMNH D 24168; 1 ♂ [2.6], 1 ♀ [2.3], 1 intersex [1.9], 58°16'N, 11°29'E, 20-30 m, 15.ix.1965, RMNH D 24171; **Denmark:** 13 ♂♂ [2.2-2.8], 4 ovig. [1.9-2.8], off Lilla Middelgrund, 29.3-31.1 m, sandy bottom, 10.vii.1878, collector Théel, NHRM 2240; 1 ♂ [1.6] off Torrboskär-Skagen, 49.4 m, sandy bottom, 8.vii.1878, collector Théel, NHRM 2245; 2 ovig. [1.6, 1.9], off Skagen-Nidingarna, 34.7 m, bottom of gravel and stones, 9.vii.1878, collector Théel, NHRM 2246; 1 ♂ [1.7], 1 ♀ [2.6], off Aalborg-Bucht, 20-30 m, 29.vi-1.vii.1976, collector Pettke, SMF 7582; **France:** 2 ♀♀ [1.8, 2.0], "Princess Alice II" station 2974, off Belle Ile", 47°23'N, 3°25'W, 85 m, 27.vii.1910, MOM 380997; **Azores:** 2 ovig. [1.0, 1.6], "Princess Alice" station 594, off Point S. Antonio, Terceira, 54 m, rocky bottom, 22.vii.1895, MOM 380322; 3 ♂♂ [0.6-2.5], 1 ♀ [2.5], "Josephine Expedition" station d 45, off São Miguel, 9.1-18.3 m, rocky bottom, 16-17.vii.1869, NHRM 6976; 5 ♂♂ [1.4-1.7], 1 ovig. [1.4], "Josephine Expedition" station d 72 (c), off Ponta Delgada, 7.3-18.3 m, 1869, NHRM 6996; 2 ♂♂ [1.6, 1.8], "Josephine Expedition" station d 76 (b), off Ponta Delgada, 18.3 m, bottom of gravel, 1869, NHRM 6997. **Mediterranean Sea: Spain:** 1 ♂ [1.8], 1 ovig. [1.2], Bay of Cadaqués, 4-16.viii.1949, collector L.B. Holthuis, RMNH D 6774; 2 ♂♂ [1.1, 1.4], 2 ♀♀ [0.8, 0.9], 1 ovig. [1.2], Bay of Cadaqués, 20-50 m, 11-18.viii.1954, collector L.B. Holthuis, RMNH D 10284; 1 ♂ [1.3], Bay of Cadaqués, 30-40 m, 29.vii.1955, collector L.B. Holthuis, RMNH D 10913; 1 ♂ [1.7], Bay of Cadaqués, 26-31.vii.1955, collector L.B. Holthuis, RMNH D 10914; 2 ♂♂ [1.4], Bay of Cadaqués, 45 m, 1.viii.1957, collector L. B. Holthuis, RMNH D 12270; 1 ovig. [2.2], Bay of Cadaqués, up to 1 m, on seagrass bed, 31.vii.1957, collector L.B. Holthuis, RMNH D 12283; 1 ♂ [1.6], Bay of Cadaqués, 20-30 m, 14.viii.1959, collector L.B. Holthuis, RMNH D 14883; 5 ♂♂ [1.2-1.8], 1 ♀ [1.2], 1 ovig. [1.3], Bay of Cadaqués, 30-90 m, sandy bottom, 27.vii-2.viii.1961, collector L.B. Holthuis, RMNH D 16514; 5 ♂♂ [1.4-2.0], 1 ♀ [1.5], 3 ovig. [1.6-2.0], off Formentera, Balearic Islands, 64 m, 1871, collector F. Söderlund, NHRM 12058; 2 ♂♂ [1.3, 1.4], 1 ♀ [1.9], 91.4 m, 1871, collector F. Söderlund; 2 ♂♂ [2.3, 2.4], off San Antonio, Ibiza, Balearic Islands, 45.7 m, 1871, collector F. Söderlund, NHRM 12061; **France:** 4 ♂♂ [1.8-2.0], "L'Eider" station 3422, from off Beaulieu to Roquebrune-Cap-Martin, x-xi.1926, MNHN 1817; **Monaco:** 1 ♂ [2.0], off Cap d'Ail, Port-Marquet, 15 m, 17.iv.1953, collector H. Nouvel, RMNH D; **Italy:** 3 ♂♂ [2.1-2.6], off Sori, Golfo di Genova, 36.6-54.9 m, coralline bottom, 3.x.1887, collector Théel, NHRM 10575; 1 ♂ [2.4], off Naples, 7.xii.1937, MOM 382514; 1 ♂ [2.0], 1 ovig. [2.0], off Naples, 7.xii.1937, MOM 382515; 1 ♂ [1.3], Golfo di Taranto station 308, 39 m, sandy bottom, 26.viii.1966, collector A. Vatova, RMNH D 24174; **Yugoslavia:** 1 ovig. [1.7], off Rovinj, 20 m, 15.viii.1960, RMNH D 16159; 1 ♂ [2.2], off Rovinj, 32-38 m, 3.vi.1962, RMNH D 19430; 1 ovig. [1.8], off Rovinj, 32-38 m, 2.vi.1962, RMNH D 19435; **Strait of Sicily:** 12 ♂♂ [1.9-2.5], 1 ♀ [2.4], 3 ovig. [2.0-2.1], "AAK" station 1261, 37°26.8'N, 12°11.6'E, 57 m, bottom of sand and clay, 24.iv.1978, collector V.V. Murina, MMSU; 2 ♂♂ [1.9, 2.8], "AAK" station 1262/55, 37°40.0'N, 12°03.0'E, 21 m, bottom of clay and sand, 24.iv.1978, collector V.V. Murina, MMSU; 6 ♂♂ [1.6-2.2], 1 ♀ [2.0], 1 ovig. [1.5], "AAK" station 1265, 35°27.0'N, 11°39.3'E, 70 m, bottom of clay and sand, 26.iv.1978, collector V.V. Murina, MMSU; 1 ♂ [1.8], 1 ovig. [1.9], "AAK" station 1266/63, 35°22.0'N, 11°44.2'E, 65 m, sandy bottom, 26.iv.1978, collector V. V. Murina, MMSU; 2 ♂♂ [1.5, 1.8], 1 ♀ [1.9], 1 ovig. [1.5], "AAK" station 1267, 35°10.0'N, 12°14.4'E, 50 m, bottom of sand and algae, 27.iv.1978, collector V.V. Murina, MMSU; 2 ♂♂ [2.0, 2.2], "AAK" station 1268, 35°10.8'N, 12°34.0'E, 47-50 m, sandy bottom, 27.iv.1978, collector V.V. Murina, MMSU; 8 ♂♂ [1.9-2.6], 3 ovig. [1.7-2.0], "AAK" station 1269/70, 35°13.0'N, 12°38.5'E, 57 m, sandy bottom, 28.iv.1978, collector V.V. Murina, MMSU; 2 ♂♂ [2.1, 2.2], 1 ovig. [1.9], "AAK" station 1273/82, 35°56.3'N, 15°00.0'E, 91 m, bottom of sand and shells, 30.iv.1978, collector V.V. Murina, MMSU; 2 ♂♂ [1.9, 2.0], "AAK" station 1288, 35°38.8'N, 15°1.7'E, 97 m, bottom of clay and sand, 2.ix.1979, collector V.V. Murina, MMSU; 2 ♂♂ [1.8, 1.9], "AAK" station 1295, 35°22.7'N, 15°06.8'E, 80 m, bottom of clay and sand, 4.ix.1979, collectors V.V. Murina & V.D. Tchukhtchin, MMSU; 1 ♂ [2.0], 1 ♀ [1.9], "AAK" station 1296, 37°30.7'N, 12°06.5'E, 86 m, sandy bottom, 10.ix.1979, collectors V.V. Murina & V.D. Tchukhtchin, MMSU; 2 ♂♂ [2.2, 2.5],

"AAK" station 1297, 37°28.9'N, 12°12.0'E, 62 m, sandy bottom, 11.ix.1979, collectors V.V. Murina & V.D. Tchukhtchin, MMSU; 1 ovig. [2.7], "AAK" station 1299 (42/4), 37°28.9'N, 12°12.0'E, 62 m, sandy bottom, 11.ix.1979, collectors V.V. Murina & V.D. Tchukhtchin, MMSU; 1 ♂ [2.0], "AAK" station 1311/57, 35°09.2'N, 12°28.2'E, 48 m, sandy bottom, 17.ix.1979, collector V.V. Murina, MMSU; 17 ♂♂ [1.6-2.1], 5 ♀♀ [1.5-2.0], 4 ovig. [1.5-1.7], "AAK" station 1313, 35°17.2'N, 12°04.5'E, 53 m, bottom of sand and *Udotea*, 17.ix.1979, collector V.V. Murina, MMSU; 1 ♂ [1.9], 2 ovig. [1.5, 1.7], "AAK" station 1390, 35°18.3'N, 12°04.4'E, 55 m, sandy bottom, 2.ix.1980, collector V.V. Murina, MMSU; 1 ♂ [1.4], "AAK" station 1392, 35°30.7'N, 12°01.2'E, 72 m, bottom of sand and *Lithothamnium*, 3.ix.1980, collectors V.V. Murina & V.D. Tchukhtchin, MMSU; 1 ♂ [2.3], 1 ♀ [1.8], "AAK" station 1394, 60 m, sandy bottom, 6.ix.1980, collectors V.V. Murina & V.D. Tchukhtchin, MMSU; 3 ♂♂ [1.9-2.3], "AAK" station 1397, 37°19.3'N, 12°07.9'E, 80 m, sandy bottom, 7.ix.1980, collectors V.V. Murina & V.D. Tchukhtchin, MMSU; 1 ♂ [2.1], 2 ovig. [1.9, 2.6], "AAK" station 1398, 37°23.6'N, 12°16.5'E, 70 m, sandy bottom, 7.ix.1980, collectors V.V. Murina & V.D. Tchukhtchin, MMSU; 3 ♂♂ [1.4-2.8], "AAK" station 1400, 37°28.1'N, 12°13.5'E, 65 m, bottom of sand and dead and living corals, 8.ix.1980, collectors V.V. Murina & V.D. Tchukhtchin, MMSU. **Southeastern Atlantic: Cape Verde:** 1 ♂ [1.1], 1 ovig. [0.9], off Port Grande (= Mindelo), São Vicente, 16.5 m, 5.iii.1890, NHRM 7362; 1 ♂ [0.8], "Atlantide" station 40, Bay of São Pedro, São Vicente, 32 m, bottom of sand and foraminiferans, 11.xii.1945, ZMUC; 1 ovig. [1.2], "Atlantide" station 43, Bay of Praia, São Tiago, 8 m, bottom of sand and gray silt, 13.xii.1945, ZMUC; 1 ♂ [1.4], 1 ovig. [1.2], "Galathea" station 62, off Namibia, 22°19'N, 17°05'W, 62 m, bottom of shells and bryozoans, 2.xi.1950, ZMUC.

**Diagnosis.**— Shield slightly longer than broad. Rostrum slightly exceeding lateral projections. Lateral projections with short submarginal spine.

Ocular peduncles approximately  $\frac{4}{5}$  length of shield; with corneae slightly dilated. Ocular acicles narrowly triangular, with strong submarginal spine. Interocular plate unarmed.

Antennular peduncles exceeding distal margin of corneae by approximately entire length of ultimate segment. Ultimate antennular segment exceeding length of penultimate segment by approximately  $\frac{1}{2}$  own length, with dorsolateral row of short setae and 1 moderately long seta distally; ventral margin with row of tufts of moderately long setae; basal segment with laterodistal spine.

Antennal peduncles approximately reaching distal margin of corneae. Antennal acicles terminating in short spine reaching proximal margin of corneae.

All surfaces of right cheliped with numerous tufts of long or moderately long setae. Chela moderately narrow (males) or broad (females). Dactyl approximately  $\frac{2}{3}$  length of palm, triangular in cross section, with elevated, dorsomesial, spinulose ridge and ventromesial, granular ridge. Palm approximately  $\frac{4}{5}$  length of carpus, much narrower in males, with spinulose or granular ridge on proximal half of dorsomesial margin; dorsal surface convex, spinulose or granular, with prominent, spinulose ridge (more so in females) near dorsomesial margin proximally; dorsolateral margin with row of spinules extending onto fixed finger but becoming obsolete near claw; dorsoproximal margin with weakly developed lateral and mesial lobes; ventroproximal margin with median, subrectangular sinus. Carpus exceeding merus approximately by  $\frac{1}{4}$  own length, much shorter in females; dorsomesial margin with irregular row of closely spaced spines; dorsomesial distal angle produced into moderately large, subcircular structure with a more raised ventral side; dorsodistal margin lacking triangular projection adjacent to dorsomesial distal angle; dorsal surface granular; dorsolateral margin spinulose or granular and with 1, occasionally 2, acute spines; dorsolateral, distal angle produced into small, subcircular lobe; mesial face

slightly compressed, granular or spinulose; ventromesial margin subcircular in mesial view; ventral surface granular or spinulose and with numerous tufts of very long, stiff setae; ventral length between shallow, subcircular, ventrodistal and ventroproximal margins moderately long in males but short in females; lateral face granular or spinulose. Dorsal margin of merus with small distal spine (small specimens) or unarmed (large specimens); ventromesial margin with small distal spine (both sexes) and well-developed setose protuberance (males); ventrolateral margin with 3 to 5 strong spines; ventral surface with spinules or granules and numerous tufts of very long, stiff setae. Ischium with 1 spinule on ventrolateral margin partly covered by tufts of long, stiff setae. Coxae of chelipeds with ventrolateral, distal angle unarmed.

Dactyl of left cheliped smooth but with tufts of long setae. Dorsomesial margin of carpus with row of 4 to 6 strong, widely spaced spines; dorsolateral margin with 3 or 4 strong, widely spaced spines.

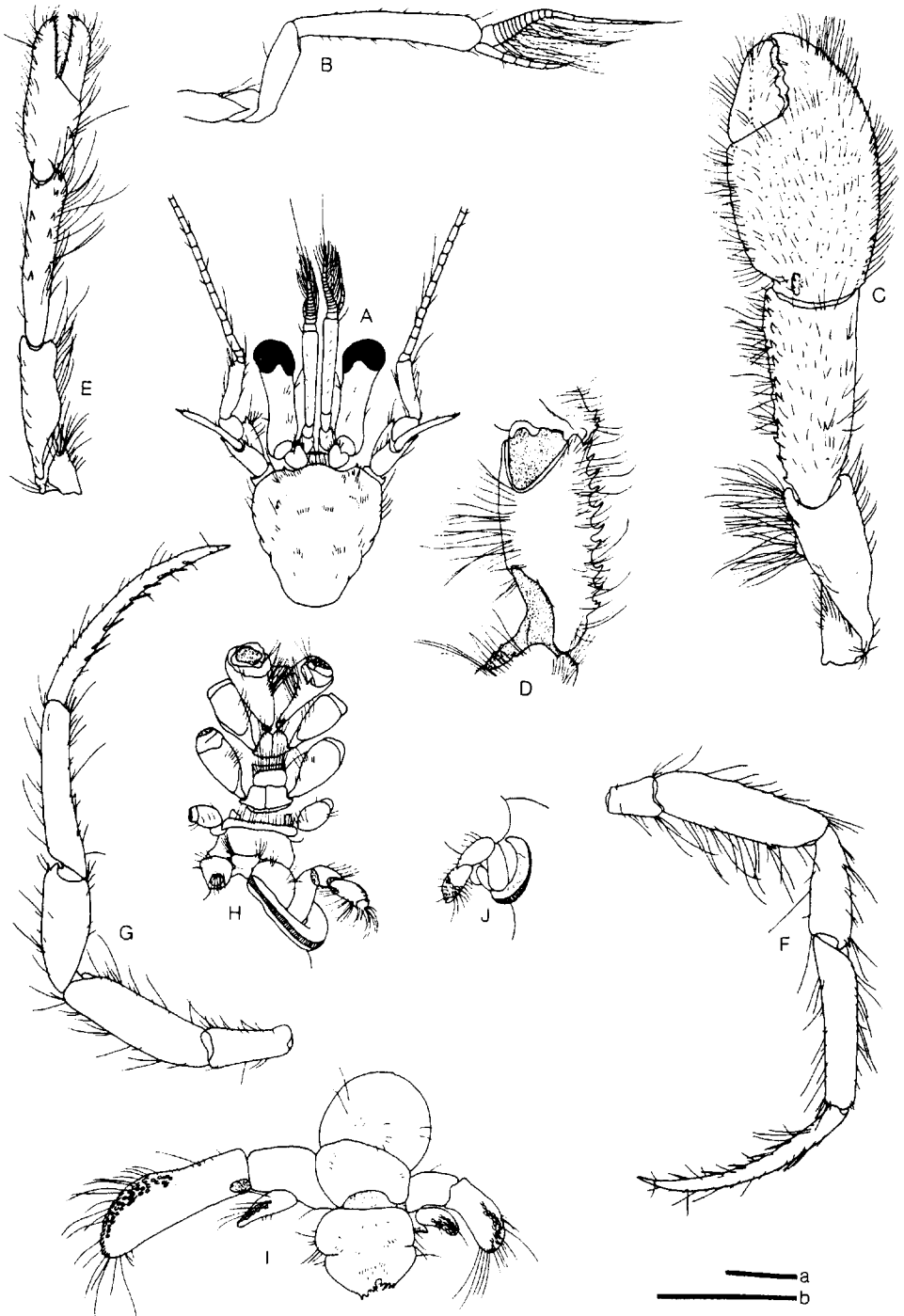
Ambulatory legs with dactyls exceeding propodi by approximately  $\frac{1}{4}$  own length, with dorsomesial row of widely spaced, moderately long, stiff setae interspersed with short setae; mesial faces each with row of widely spaced, moderately long, spine-like setae interspersed with moderately long setae near ventral margin; lateral faces each with row of widely spaced, moderately long setae near dorsal and ventral margins. Propodi exceeding carpi by approximately  $\frac{1}{3}$  own length; dorsal surfaces each with row of tufts of closely spaced, moderately long, stiff setae; mesial and lateral faces each with row of widely spaced, moderately long setae near ventral margin; ventromesial distal angle with 1 moderately long, spine-like seta. Carpi approximately  $\frac{2}{3}$  length of meri; dorsal surfaces each with row of tufts of moderately long, stiff setae and 1 proximal and 1 distal spine (2nd) or only 1 distal spine (3rd). Ventral margins of meri with row of tufts of closely spaced, long, stiff setae and 1 spinule on distal half (2nd) or unarmed (3rd). Lobes of sternite of 2nd pereopods unarmed, distally rounded. Anterior lobe of sternite of 3rd pereopods subrectangular (males) or subcircular (females); anterior margin with tufts of long setae. Males with well-developed, left sexual tube, recurved upward to level of coxa; coxa of right 5th pereopod with gonopore on distoventral surface, partly covered by tufts of moderately long setae; three uniramous pleopods. Distal protopodal lobe of right uropod less than  $\frac{1}{2}$  length of endopod.

Telson with asymmetrical posterior lobes separated by narrow, shallow cleft; terminal margins each with 3 or 4 short spines; lateral margins unarmed but with tufts of moderately long setae.

Colour.— "Colour reddish brown, uniform all over" (Norman, 1861; as *Pagurus ferrugineus*).

"...; when freshly taken it (as *Anapagurus ferrugineus*) may however be recognized by the bright colour of the antennules, the stalks of which are red, while the flagella are a brilliant blue." (Henderson, 1885).

Fig. 6. *Anapagurus chiroacanthus* (Lilljeborg, 1856). A-I: ♂ (SL = 2.5 mm), "AAK" station 1297, 37°28.9'N, 12°12.0'E, MMSU: A, shield and cephalic appendages; B, right antennule (lateral view); C, right cheliped (dorsal view); D, carpus of same (ventromesial view); E, left cheliped (dorsal view); F, left 2nd pereopod (mesial view); G, left 3rd pereopod (mesial view); H, sternum; I, extremity of abdomen, uropods, and telson. J: ♂ (SL = 2.0 mm), off Smedjebrotten, Bohuslän, NHRM 4678: left sexual tube (lateral view). Scales equal 1.0 mm: a: A, C-H, J; b: B, I.



"...; negli esemplari del golfo di Napoli (la cornea) ha colore fondamentale gialliccio, con numerose macchie circolari, di colore rosso vermiglio" (Fenizia, 1937: 29-30). (= The corneae of the specimens from the Gulf of Naples are basically yellow with numerous bright red circular spots). "Il colore generale del corpo è di un rosso più chiaro" (Fenizia, 1937: 33; as *A. chiroacanthus* var. *cristatus*). (= The general colour of the body is light red).

Behaviour.— Several aspects of the behaviour of *A. chiroacanthus* have been studied, including dislodging (Hazlett, 1968a), sexual (Hazlett, 1968b; Salmon, 1983), field patterns of shell occupancy (Hazlett, 1981), and feeding (Schembri, 1982).

Related organisms.— The specimens of *A. chiroacanthus* studied by Fenizia (1937) were found inhabiting the gastropod shells of *Turritella*, *Ziziphinus*, and *Nassa* (= *Hinia*); the shell of *Nassa incrassata* (Strom, 1768) (= *Hinia incrassata*) was covered with poriferan *Suberites*. Pike & Williamson (1958) found *A. chiroacanthus* in *Nassarius* (= *Hinia*) and *Gibbula tumida* (Montagu, 1803). In the present collections the following shells were found occupied by *A. chiroacanthus*: Cerithidae (1 specimen, MMSU-"AAK" station 1311-57); *Epitonium clathrus* (Linnaeus) (1 specimen, NHRM 1020); *Epitonium* sp. (2 specimens NHRM 452 and 494; *Gibbula pennanti* (1 specimen, RMNH D 19130; 5 specimens, NHRM 442, 443, 582, 608, and 620); *Gibbula tumida* (1 specimen, USNM 17008); *Hinia reticulata*: (33 specimens, NHRM 1414, 1429, 1542, 1872, 2246, 2549, 3223, 3519, 3682, 4173, 6996 and 6997); *Littorina* sp. (6 specimens, NHRM 1425); Naticidae (2 specimens, NHRM 1414 and 4173); *Ocinebrina aciculata* (5 specimens, NHRM 6976, 6996 and 10575); *Raphitoma linearis* (Montagu, 1803) (1 specimen, NHRM 2469); *Turritella biplicata* (2 specimens, ZMUC; 2 specimens, MMSU-"AAK" station 1390; 12 specimens, NHRM 1390, 1425, 1429, 1531, 1532, 2240, 3223, 4173, 4255 and 4261); and *Turritella communis* (2 specimens, MMSU "AAK" station 1397 and 1398; 4 specimens, NHRM 1531, 2240 and 2549).

Gastropod shells covered by poriferans [e.g., *Suberites domuncula* and/or *S. ficus* (Esper)] and inhabited by *A. chiroacanthus* have been recorded by Aurivillius (1891), Sars (1924), Balss (1956), and Füller (1958). In the present collections 21 gastropod shells occupied by *A. chiroacanthus* were covered by *S. domuncula* (NHRM 1020, 1022, 1041, 2021, 2342, 2549, 3226, 3485, 3519, 3682 and 5772). Other organisms found on shells occupied by *A. chiroacanthus* are: anthozoan *Epizoanthus* sp. (RMNH D 19426); barnacles, bryozoans, foraminiferans, hydrozoans and serpulid polychaetes (MMSU "AAK" station 1398; NHRM 4255); and *Anomia epippium* (Linnaeus), barnacles and serpulid polychaetes (NHRM 4186).

*Anapagurus chiroacanthus* has been reported as being infested by two bopyrid isopods, *Pseudione hyndmanni* by Pike (1961), Bourdon (1968), and Markham (1986), and *Athelges tenuicaudis* Sars, 1899, by Elmhirst (1912), Thorson (1946), and Pike (1950, 1961). During the present study, only 9 specimens of the abdominal parasite, *Athelges tenuicaudis* have been found in *A. chiroacanthus* (NHRM 1020, 1021, 1429, 4261 and 4677). One of the females infested (NHRM 1429: SL= 2.0 mm) lacks the right gonopore, and one intersex specimen (NHRM 4677: SL= 1.9 mm) lacks the gonopores and the sexual tube. The other hosts show no external changes.

Two species of rhizocephalans, *Peltogaster paguri* and *Peltogasterella sulcata*, have been recorded as parasites of *A. chiroacanthus* by Balss (1926), Buddenbrock (1948), Høeg & Lützen (1985), Nilsson-Cantell (1926) and Reinhard (1942). The last two

authors described the effects of these parasites in *A. chiroacanthus*. In the present collections, one, and occasionally two, externae per host of *P. paguri* have been found in 31 specimens of *A. chiroacanthus* (MMSU "AAK" stations 1268, 1313 and 1390; RMNH D 19131, 19425, 19431, 19433 and 24171; NHRM 1020, 1022, 1414, 1425, 1427, 1428, 1429, 1531, 3227, 3484, 4255, 4261 and 4678). Eight *A. chiroacanthus* were found with 2-6 externae of *P. sulcata* per host (NHRM 1022, 1428, 1429, 1872, 2549, 2758 and 4678). Most parasitized specimens had varying degrees of changes in the presumed secondary sexual characteristics, such as the absence of pleopods 2 and 3 (under the externae), the feminization of the male pleopods, the reduction or absence of sexual tubes and lack of female gonopores.

Two ovigerous females of *A. chiroacanthus* collected off Tunisia (MMSU "AAK" station 1269-70) had 1 or 2 folliculinid protozoans type 1 (see section on related organisms for *A. hyndmanni*) attached to their abdomens dorsally. This is the first record of folliculinids infesting *A. chiroacanthus*.

On 54 specimens of *A. chiroacanthus* collected in the Kattegat waters (NHRM 1429, 1436, 1532, 1538, 2240, 2250, 2549, 2642, 3224, 3225, 3227, 3484, 3682, 3685, 3686, 4255, 4256, 4261, 4676, 4677 and 4678) and 1 off Ponta Delgada, Azores (NHRM 6996), there were foraminiferans. They usually ranged in number from 1 to 3 tests, occasionally 6 and 9; most tests are attached dorsally to the carpus and palm of the right cheliped and on the shield of the hosts. Occasionally they are found dorsally on the carpus of left cheliped and walking legs. This kind of association with foraminiferans is the first record for the genus *Anapagurus*.

Life history.— Larvae of *A. chiroacanthus* have been studied by Bouvier (1891), Gurney (1942), Thorson (1946), MacDonald, Pike & Williamson (1957), Pike & Williamson (1958, 1960), and Calafiore (1981). Ingle (1990) provided the description of its complete larval and post-larval development. Thorson (1946), and Pike & Williamson (1959) covered the breeding aspect of this species.

Distribution.— *A. chiroacanthus* has been recorded in the northeastern Atlantic from Raunefjorden, southwest of Bergen, Norway (Lagerberg, 1908; Samuelsen, 1970) to off Cape Verde Islands (Forest, 1961). Lilljeborg (1856) described this species as *Pagurus chiroacanthus* found off Kullaberg, southwest of Sweden. This species has also been recorded from the British Seas by Norman (1861; as *Pagurus ferrugineus*), Henderson (1886; as *P. ferrugineus*), Norman (1911), Elmhirst (1912), and Pike & Williamson (1959); off the Azores (A. Milne-Edwards & Bouvier, 1899; as *A. brevicarpus*); off Portugal (Neves, 1977); off Cape Bojador, Morocco (Forest, 1955) and off Rio de Oro (21°30'N, 17°05'W; Forest, 1961).

Additionally, the species has been recorded in the Mediterranean Sea: off the Balearic Islands (Forest, 1965), Bahía de Cadaqués and off Cabo de Creus (Zariquiey Alvarez, 1955, 1968), Golfo di Napoli (Balss, 1926; Fenizia, 1937), and in the Aegean Sea, off Turkey (Kocatas, 1981).

The specimen collected off Trondheimsfjorden (63°42'N, 9°27'E); west Norway; RMNH D 24170) extends the northern range of the species. All localities off the coasts of Denmark, France, Monaco, Yugoslavia, Gulf di Taranto and Strait of Sicily are new records for *A. chiroacanthus*. Depth range: 0-200 m; most frequently found in depths of 10 to 60 m.

Affinities.— *Anapagurus chiroacanthus* is similar to *A. japonicus*, sharing the dorso-

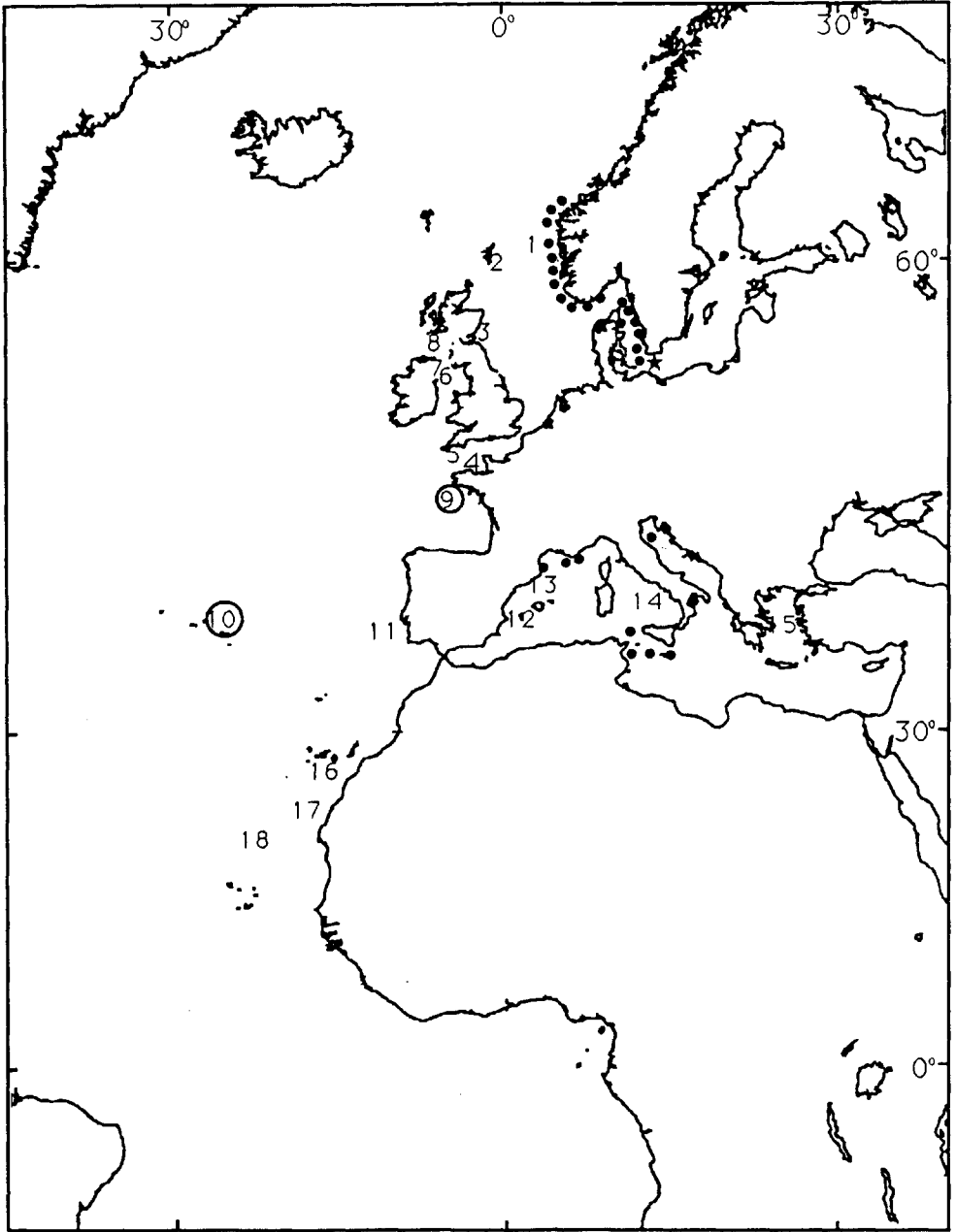


Fig. 7. Distribution of *Anapagurus chiroacanthus* (Lilljeborg, 1856) Star: type locality. Solid circles: based on present records. Numbers: based on previous records (circled numbers: material examined): 1-Samuelsen, 1970; 2, 4, 7-Norman, 1861; 3-Norman, 1911; 5, 6, 8-Pike & Williamson, 1959; 7-Henderson, 1886; Elmhirst, 1912; 9-Bouvier, 1922; 10-A. Milne Edwards & Bouvier, 1899; 11-Neves, 1977; 12-Forest, 1965; 13-Zariquiey Alvarez, 1955; 1968; 14-Balss, 1926; Fenizia, 1937; 15-Kocatas, 1981; 16-Forest, 1955; 17, 18-Forest, 1961.



mesial and ventrolateral ridges of the dactyl of the right chela, and in males three uniramous pleopods. *Anapagurus chiroacanthus* can be separated from *A. japonicus* by the more setose chelipeds and walking legs, the spinose, dorsolateral margin of left cheliped, the much shorter but more numerous spines of the terminal margins of the telson, and in males the much longer, ventrocarpal length of the right cheliped.

*Anapagurus chiroacanthus* shares the setose appearance of *A. hendersoni* but the former species can be distinguished by the weaker armature of the chelipeds, walking legs, and telson, and the male uniramous pleopods 3 and 4.

Remarks.— Among specimens collected off Kullaberg, Skåne (southwestern Sweden), Lilljeborg (1856) had specimens that he described as *Pagurus chiroacanthus*. Norman (1861), studying the British crustaceans, described a new species, *Pagurus ferrugineus*, which he compared with the British congeners, *P. cuanensis*, *P. thomsoni* (= *P. pubescens*) and *P. laevis*. Previous to this latter work, Stimpson (1858) had erected *Spiropagurus*, the first pagurid genus with extruded vas deferens, so Norman either ignored the Stimpson's taxon, examined only females or simply overlooked the presence of sexual tube(s).

A. Milne Edwards & Bouvier (1892), briefly described *A. brevicarpus* based on two female specimens collected at different localities [north of Spain (170 m) and north of Arguin Bank (135-250 m)]. In 1900, these authors more completely described and illustrated this species. Forest (1961) reexamined the remains (right cheliped, left 3rd pereopod, and abdomen) of the syntype female collected north of Spain ("Travailleur" station 5, 43°59'N, 8°59'W, 170 m, silty bottom, 9.vii.1882, MNHN?) and, together with A. Milne Edwards and Bouvier's illustrations (1900: pl XXV: figs. 23-26, and pl. XXVIII: fig. 11), questionably considered *A. brevicarpus* a junior synonym of *A. chiroacanthus*.

The present extensive collections of *A. chiroacanthus*, which comprise nearly one thousand specimens, have revealed that among other characters, the right cheliped displays strong, morphological and morphometric sexual dimorphisms (e.g. in males the much narrower palm with less developed ridge near mesial margin proximally, and in females the much shorter carpus). Furthermore, I have had the opportunity to reexamine the following specimens (all females) of *A. brevicarpus* from reported collections: (1) the remains (right 2nd and 3rd pereopods) of the other syntype specimen collected north of Arguin Bank ("Talisman" station 90, 21°51'N, 19°48'W, 135-250 m, bottom of greenish sand and silt, 13.vii.1883, MCZ 6579); (2) the specimen reported by A. Milne Edwards & Bouvier (1899) collected off Ponta do São Antonio, Terceira, Azores ("Princess Alice" station 594, 54 m, rocky bottom, 22.vii.1895, MOM 380322); and (3) the specimen cited by Bouvier (1922) and collected off Paragés de Belle Ile ("Princess Alice II" station 2974, 47°23'N, 3°25'W, 85 m, plateau bottom, 27.vii.1910, MOM 380997). I have concluded that all of these specimens are conspecific with *A. chiroacanthus*.

The specimens that Mouchet (1931) used in her studies of the spermatophores of *A. brevicarpus*, and those reported by Cardona Bendito (1965) from Ría de Vigo, Spain, have not been available for examination, and therefore are questionably considered conspecific with *A. chiroacanthus*.

*Anapagurus pusillus* Henderson, 1888, sensu stricto  
(figs. 8, 9)

*Anapagurus pusillus* Henderson, 1888: 73 (in part), pl. VII: fig. 7 (type locality, herein restricted by lectotype selection: "Challenger" station VII p, 28°35'00"N, 16°05'00"W, off Gomera Island, Canary Island, 143 m, bottom of volcanic sand); Alcock, 1905: 187 (in part); Balss, 1924: 768; Monod, 1932: 487 (in part); Gordan, 1956: 303 (in part; see remarks).

not *Anapagurus pusillus*; Stebbing, 1910: 358 (= *A. hendersoni* Barnard, 1947); Balss, 1912: 110 (= *A. hendersoni* Barnard, 1947); Odhner, 1923: 13 (= *A. longispina* A. Milne-Edwards & Bouvier, 1900) (see remarks).

*Anapagurus laevis*; Forest, 1955: 131 (in part; see remarks).

Material.— Lectotype herein selected: ♂ [2.1], off Gomera Island, Canary Islands, "Challenger" station VII p: 28°35'00"N, 16°05'00"W, 143 m, bottom of volcanic sand, 10.ii.1873, BMNH 1888: 33; Paralectotypes: 2 ♂♂ [1.5, 1.7], 1 ♀ [1.7], 2 ovig. [1.7, 1.8], data as for lectotype. Off Azores: 1 ♀ [1.7], "Josephine Expedition" station e16, off Villa Franca, São Miguel, 54.9-91.4 m, bottom of gravel, 26.vii.1869, NHRM 6978; 1 ♂ [1.5], 1 ♀ [0.7], 2 ovig. [1.0, 1.6], "Josephine Expedition" station e54 (g), off Faial, up to 27.4 m, 1869, NHRM 6986; 2 ♂♂ [1.2, 2.6], 1 ♀ [2.3], 5 ovig. [1.7-2.0], "Josephine Expedition" station e62 (a), off Faial, 54.9-146.3 m, bottom of black gravel and shells, 3.viii.1869, NHRM 6989; 1 ovig. [0.9], "Josephine Expedition" station d 68 (c), 18.3m, bottom of gravel, 1869, NHRM 6995. Off S Portugal: 1 ovig. [3.0], Ria de Faro, near Cabo de Arnel, 29.vii.1962, RMNH D 19365.

Diagnosis.— Shield broader than long. Rostrum slightly overreached by lateral projections. Lateral projections with short, submarginal spine.

Ocular peduncles  $\frac{2}{3}$  to  $\frac{3}{4}$  length of shield; with corneae moderately dilated. Ocular acicles roundly triangular, with strong submarginal spine. Interocular plate unarmed.

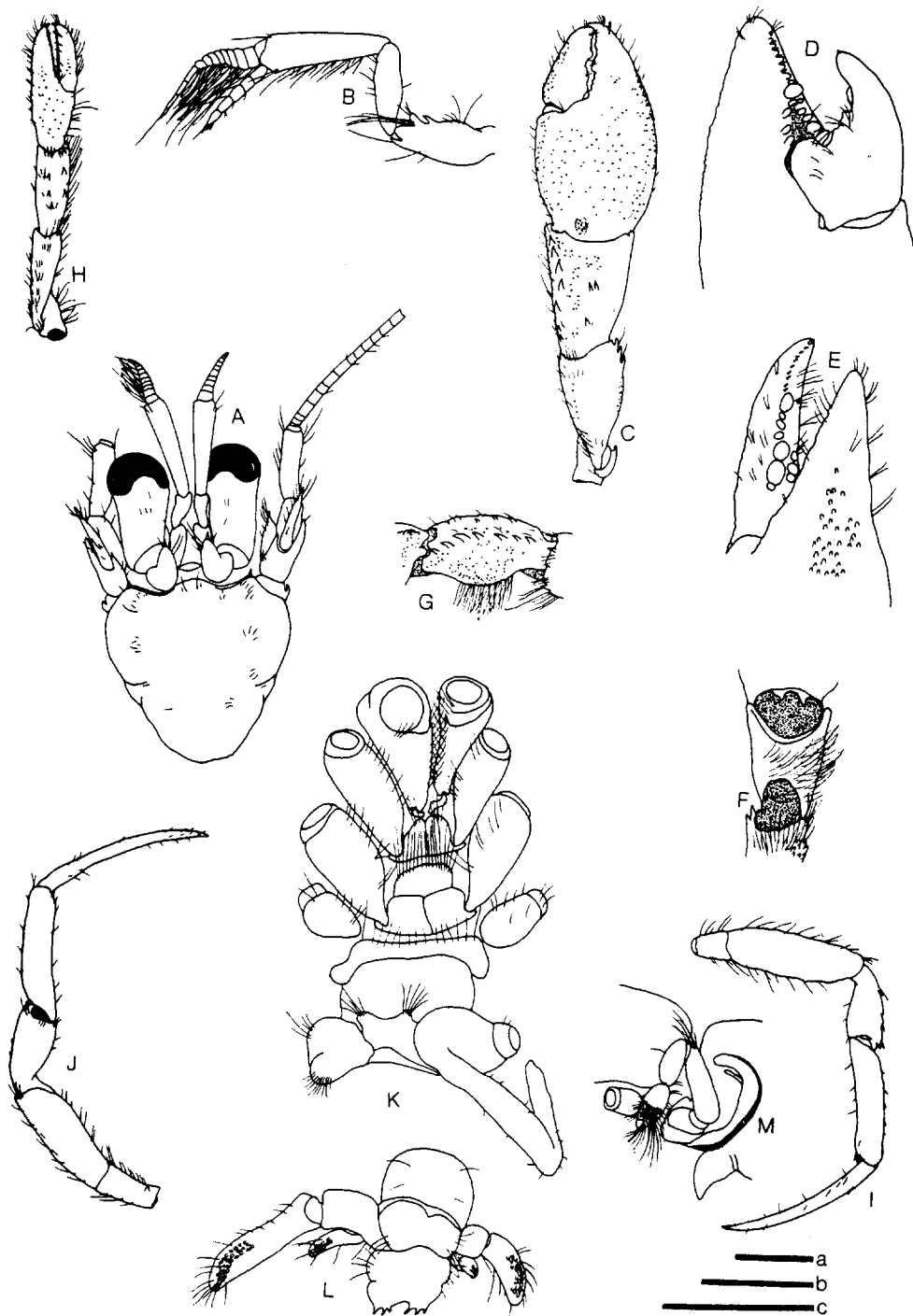
Antennular peduncles exceeding distal margins of corneae by approximately  $\frac{1}{2}$  length of ultimate segment. Ultimate segment exceeding length of penultimate segment by  $\frac{1}{4}$  own length, with 1 long and 1 short seta on dorsolateral, distal angle; ventral margin with row of tufts of long setae; basal segment with lateromedial and laterodistal spines.

Antennal peduncles overreaching ocular peduncles by approximately  $\frac{1}{3}$  length of ultimate segment. Antennal acicles usually not reaching corneae proximally.

Right cheliped with moderately broad chela. Dactyl  $\frac{2}{3}$  to  $\frac{3}{4}$  length of palm; dorsomesial margin with row of tubercles or spinules; all surfaces with tufts of short setae. Palm slightly longer than carpus; dorsomesial margin with slightly developed ridge on proximal half with row of closely spaced tubercles and tufts of short setae; dorsal surface convex, with scattered granules and tufts of short setae, and short, tuberculate ridge near dorsomesial margin proximally; dorsolateral margin with spinules increasing in size on fixed finger but not extending to claw; dorsoproximal

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Fig. 8. *Anapagurus pusillus* Henderson, 1888. Lectotype ♂ (SL = 2.1 mm), BMNH-1888: 33: A, shield and cephalic appendages; B, left antennule (lateral view); C, right cheliped (dorsal view); D, fingers of same showing dentition of fixed finger; E, fingers of same showing dentition of dactyl; F, carpus of same (ventral view); G, carpus of same (mesial view); H, left cheliped (dorsal view); I, left 2nd pereopod (mesial view); J, left 3rd pereopod (mesial view); K, sternum; L, extremity of abdomen, uropods, and telson. M: ♂ (SL = 2.6 mm), "Josephine Expedition" station e 62(a), off Faial, Azores, NHRM 6989: left sexual tube (lateral view). Scales equal 1.0 mm: a: C, F-J, M; b: A; c: B, D, E, K, L.



margin with weakly developed, mesial and lateral lobes; ventroproximal margin with a slightly calcified, subcircular sinus on either side of median, skewed, subquadrate sinus. Carpus equaling or slightly exceeding length of merus; dorsomesial margin with row of strong acute spines; dorsomesial, distal angle produced into concave, subrectangular structure; dorsodistal margin with triangular projection adjacent to dorsomesial distal angle; dorsolateral margin with row of spinules; lateral face unarmed; ventromesial margin subcircular in mesial view; ventral surface with tufts of stiff setae, long in males, short in females; short ventral length between deep, subtriangular, ventrodistal margin and subcircular, ventroproximal margin. Ventromesial margin of merus with tuberculate protuberance (males) or tubercles (females); ventral surface with tubercles, setation denser and longer in males; dorsal margin with acute, distal spine. Coxae of chelipeds with ventrolateral, distal angle unarmed.

Dactyl of left cheliped smooth but with tufts of moderately long setae. Dorsomesial and dorsolateral margins of carpus, each with 3 or 4 strong, widely spaced spines.

Dactyls of ambulatory legs exceeding propodi by approximately  $\frac{1}{4}$  their own length, with dorsomesial and ventromesial rows of widely spaced, short, stiff setae. Propodi exceeding carpi by  $\frac{1}{3}$  own length; ventromesial distal angle with 1 or 2 spines (2nd) or unarmed (3rd). Carpi  $\frac{1}{2}$  to  $\frac{2}{3}$  length of meri; dorsal margins with 2-4 spines (2nd) or single, distal spine (3rd). Meri unarmed. Lobes of sternite of 2nd pereopods unarmed, distally rounded. Anterior lobe of sternite of 3rd pereopods broadly subrectangular, slightly skewed to left.

Males with moderately long and slender, left sexual tube, recurved upward to exterior, and vestigial right sexual tube; pleopods 3 and 4 unequally biramous, pleopod 5 uniramous. Distal protopodal lobe of right uropod approximately  $\frac{1}{2}$  length of endopod.

Telson with posterior, asymmetrical lobes, separated by wide, shallow cleft; terminal margins each with 3 or 4 short spines.

Colour.— Unknown.

Related organisms.— "The majority (of the specimens were) firmly ensconced in shells of *Turritella bicingulata*, Lam., one individual in a shell of *Nassa limata*, Chem." (Henderson, 1888: 74). In the present collections, specimens of *A. pusillus* were found inhabiting the following gastropod shells: *Natica catena* (4 specimens, NHRM 6986 and 6989); *Calliostoma zizyphinum* (Linnaeus, 1758) (2 specimens, NHRM 6986); *Hinia reticulata* (3 specimens, two of the shells partly covered with bryozoans and serpulid polychaetes, NHRM 6989); and *Cerithiopsis tubercularis?* (Montagu) (1 specimen, NHRM 6995).

Distribution.— Besides the type locality, *Anapagurus pusillus* has been collected off the Azores and off the south coast of Portugal. Depth range: 0-146.3 m.

Affinities.— *Anapagurus pusillus* is most closely allied to *A. breviaculeatus* and *A. alboranensis* spec. nov.. The much broader shield and much shorter, ultimate antennular segment with heavily setose ventral margin easily distinguish *A. pusillus* from *A. breviaculeatus* and *A. alboranensis* spec. nov.

Remarks.— Henderson (1888) described *A. pusillus* using specimens from the Azores and Gomera (Canary Islands). He also referred a male specimen from Simon's Bay (False Bay, South Africa) with "some hesitation" to this species. Barnard (1947)

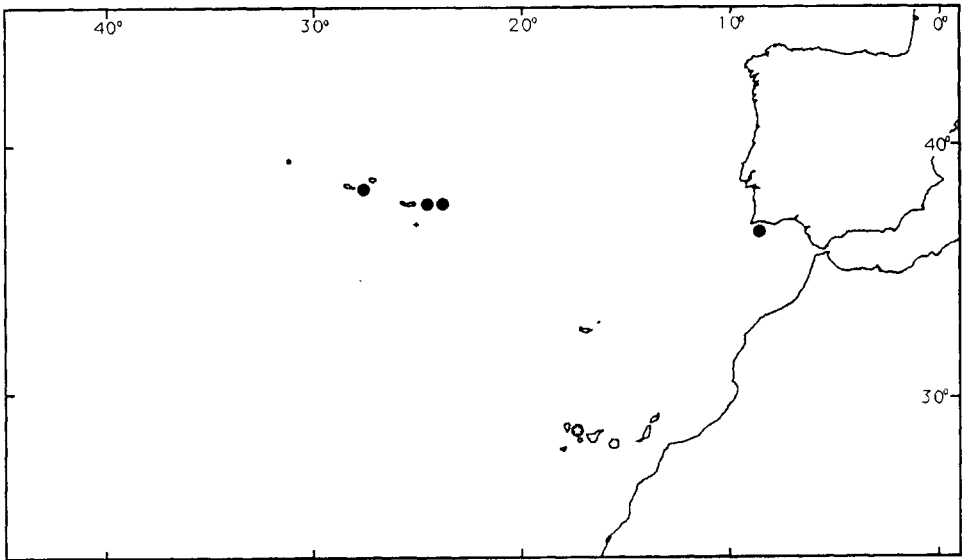


Fig. 9. Distribution of *Anapagurus pusillus* Henderson, 1888. Circled star: type locality, material examined. Solid circles: based on present records.

examined the Simon's Bay specimen, decided it was distinct from Henderson's taxon, and described it as a new species, *A. hendersoni*.

Stebbing (1910) quoted Henderson's (1888) description of *A. pusillus* when referring to the Simon's Bay specimen. As previously indicated, Barnard (1947) demonstrated that this specimen was distinct from *A. pusillus*. Balls (1912) reported *A. pusillus* from two specimens collected by the Valdivia off Cape Saint Francis, South Africa. My examinations of these specimens show that they belong to *A. hendersoni*. My examination of a female specimen from Port Alexander, Angola, identified by Odhner in 1923 as *A. pusillus*, shows that it belongs to *A. longispina*.

Forest (1955) identified specimens from the southwestern coast of Africa collected during expeditions of the "Mbizi" and "Mercator" as *A. laevis*. After examining Henderson's (1888) specimens of *A. pusillus* from the Azores and Canary Islands, Forest (1955) concluded that these too represented *A. laevis* and placed Henderson's (1888) taxon in synonymy. He did, however, concur with Barnard (1947) that Henderson's (1888) Simon's Bay specimen represented a distinct species. Having personally reexamined this specimen, I agree that it was appropriately designated a separate species. It agrees well with Barnard's (1950) supplemental material from the area, excepting one ovigerous female that represents an unidentified species of *Pagurus*. However, reexamination of Henderson's (1888) specimens from the Canary Islands has convinced me that they are not conspecific with *A. laevis*. Although I have not examined Henderson's material from the Azores, *A. pusillus* is reinstated, based upon the lectotype and paralectotypes herein designated.

The listings of Alcock (1905), Monod (1932), and Gordan (1956) included two species under the name *A. pusillus*.

*Anapagurus japonicus* Ortmann, 1892  
(figs. 10, 11)

*Anapagurus pusillus* var. *japonica* Ortmann, 1892: 296, pl.12: fig. 11 [type locality: Kadsiyama (Katsuyama), Uraga Strait, Japan, 73 m].

*Anapagurus pusillus* var. *japonicus*; Alcock, 1905: 187 (listed); Gordan, 1956: 303 (listed).

*Anapagurus japonicus*; Miyake, 1961: 24; 1978: 139, fig. 55; Miyake, Sakai & Nishikawa, 1962: 126 (listed).

*Anapagurus japonicus*; Miyake, 1965: 648, fig. 1099 (misspelling of *A. japonicus*)

Material.— Holotype: ♂, Kadsiyama (Katsuyama, Uraga Strait), Honshu, Japan, 73 m, 1880, collector Döderlein, unknown deposition; not examined. **Japan:** 1 ♂ [1.9], off Uzé, Tomioka, Kumamoto Prefecture, Kyushu, 29.v.1967, collector T. Fujino, ZLKU 11976; 1 ♀ [1.3], Kushimotochô, Wakayama Prefecture, Honshu, iii.1977, collector H. Uchida, OMNH Ar 2127.

Diagnosis.— Shield approximately as long as broad. Rostrum approximately equaling lateral projections. Lateral projections with short submarginal spine.

Ocular peduncles approximately  $\frac{3}{4}$  length of shield, with corneae slightly dilated. Ocular acicles broadly triangular, with strong submarginal spine. Interocular plate unarmed.

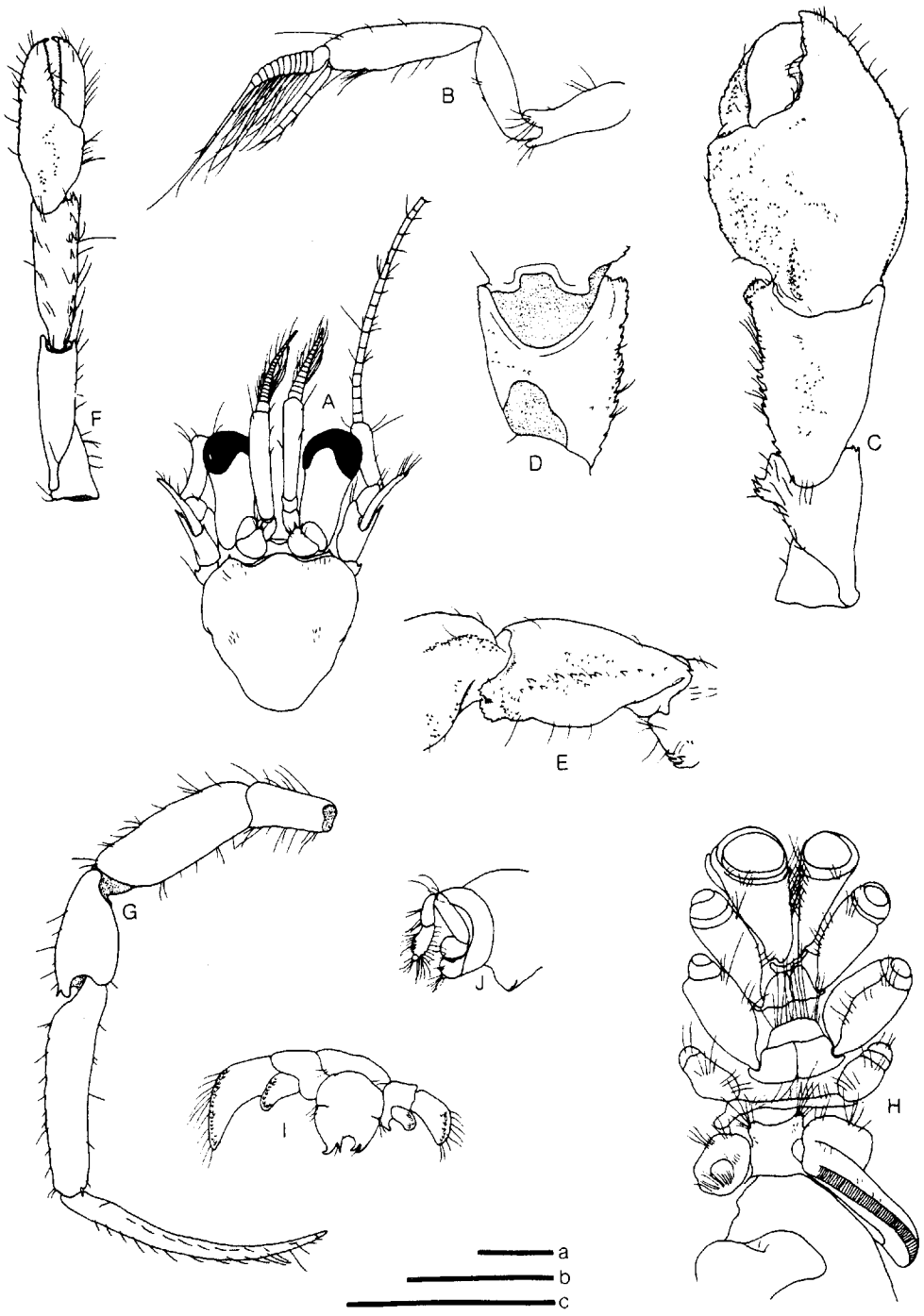
Antennular peduncles overreaching ocular peduncles by approximately entire length of ultimate segment. Ultimate segment exceeding length of penultimate segment of approximately  $\frac{1}{3}$  own length, with dorsolateral row of short setae and 2 laterodistal setae, 1 long and 1 short, ventral margin with row of moderately long setae.

Antennal peduncles slightly exceeding length of ocular peduncles. Antennal acicles overreaching proximal margin of corneae.

Right cheliped massive, with broadly oval chela. Dactyl approximately  $\frac{1}{2}$  length of palm, triangular in cross section, with elevated, dorsomedial, granular ridge and ventromesial, spinulose ridge, all surfaces granular and with tufts of short setae. Palm slightly longer than carpus, dorsomesial margin with well-developed spinulose ridge on proximal half; dorsal surface convex, with spinules (more numerous and larger near mesial margin), and very long and prominent, granular ridge near mesial margin proximally; dorsolateral margin with row of granules not extending to claw; dorsoproximal margin without mesial and lateral lobes; ventroproximal margin with skewed, median, subrectangular sinus; all surfaces with scattered tufts of short setae. Carpus exceeding merus by  $\frac{1}{3}$  of its own length, inflated, semicircular ventrally; dorsomesial margin with irregular row of closely spaced spines and spinules and moderately long setae; dorsomesial, distal angle produced into very large, spinulose, concave, subrectangular structure; dorsodistal margin lacking triangular projection adjacent to dorsomesial, distal angle; dorsal surface spinulose; dorsolateral margin unarmed but with row of widely spaced, short, stiff setae; dorsolateral,

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Fig. 10. *Anapagurus japonicus* Ortmann, 1892. ♂ (SL = 1.9 mm), off Uzé, Kyushu, Japan, ZLKU 11976: A, shield and cephalic appendages; B, left antennule (lateral view); C, right cheliped (dorsal view); D, carpus of same (ventral view); E, carpus of same (mesial view); F, left cheliped (dorsal view); G, right 3rd pereopod (mesial view); H, sternum; I, extremity of abdomen, uropods and telson; J, left sexual tube (lateral view). Scales equal 1.0 mm: a: J; b: A, C-I; c: B.



distal angle produced into small lobe; mesial face compressed, spinulose and with moderately long setae; ventromesial margin semicircular in mesial view; ventral surface spinulose and with tufts of moderately long setae; very short ventral length between deep, subtriangular, ventrodiscal margin and deep, subcircular, ventroproximal margin; lateral face convex, spinulose. Dorsal margin of merus with row of tufts of moderately long setae and partially obscured distal spines; ventromesial margin spinulose (females) or with prominent, spinose protuberance (males); ventrolateral margin with 3 or 4 strong spines; ventral surface with spinules and scattered tufts of moderately long setae. Ischium unarmed but with scattered tufts of short setae. Coxae of chelipeds with ventrolateral, distal angle unarmed.

Dactyl of left cheliped smooth but with tufts of moderately long setae. Dorsomesial margin of carpus with 6 or 7 strong closely spaced spines; dorsolateral margin unarmed.

Right 3rd pereopod of one male (ZLKU 11976) (only ambulatory leg examined) with dactyl exceeding propodus by approximately  $\frac{1}{6}$  own length, with mesial face with row of closely spaced, moderately long, stiff setae near dorsal and ventral margins; lateral face with row of widely spaced, short setae near dorsal and ventral margins. Propodus exceeding carpus  $\frac{1}{2}$  own length; dorsal surface with row of tufts of short setae; mesial and lateral faces each with row of short setae near ventral margin; ventromesial, distal angle with short spine and tuft of short setae. Carpus approximately  $\frac{2}{3}$  length of merus; dorsal surface with row of moderately long setae terminating in strong spine. Merus unarmed but dorsal and ventral surfaces each with tufts of moderately long setae. Lobes of sternite of 2nd pereopods unarmed, distally rounded. Anterior lobe of sternite of 3rd pereopods trapezoidal; anterior margin with tufts of long setae.

Male with left sexual recurved upward to level posterior carapace distally; coxa of 5th right pereopod with gonopore on distoventral surface, obscured by tufts of moderately long setae; three uniramous pleopods. Distal protopodal lobe of right uropod approximately  $\frac{1}{2}$  length of endopod.

Telson with asymmetrical, posterior lobes separated by wide, shallow cleft; terminal margins each with 2 strong spines; lateral margins unarmed but with tufts of moderately long setae.

Colour.—“(in formalin). Body and legs uniformly light yellow-brown” (Miyake, 1978: 141).

Related organisms.— The male holotype was found inhabiting a trochid shell of *Ziziphinus unicus* Dunker (Ortmann, 1892: 297). Miyake (1978), in his study of the Anomura of Sagami Bay, recorded a male *A. japonicus* inhabiting the gastropod shell of *Lancea* (= *Scaliola*) *bella* A. Adams; the hermit crab was infested with a bopyrid isopod in the right branchial chamber. He also found two males in the gastropod shells of *Minolia punctata* A. Adams and *Dimidacus stramineus* (Gray). In the present collection, an undetermined bopyrid isopod was found within the right branchial chamber of a female *A. japonicus* (OMNH Ar 2127). Except for the typical swelling of the branchiostegite, no other external changes in the host were observed.

Distribution.— *Anapagurus japonicus*, an apparently endemic Japanese species, has been recorded by Miyake (1961, 1965, 1978) off Amakusa, Western Kyushu (20–50 m), Chijiwa Bay, Nagasaki-ken (27–72 m), off Tsuyazaki, Sea of Genkai (28–39 m), and



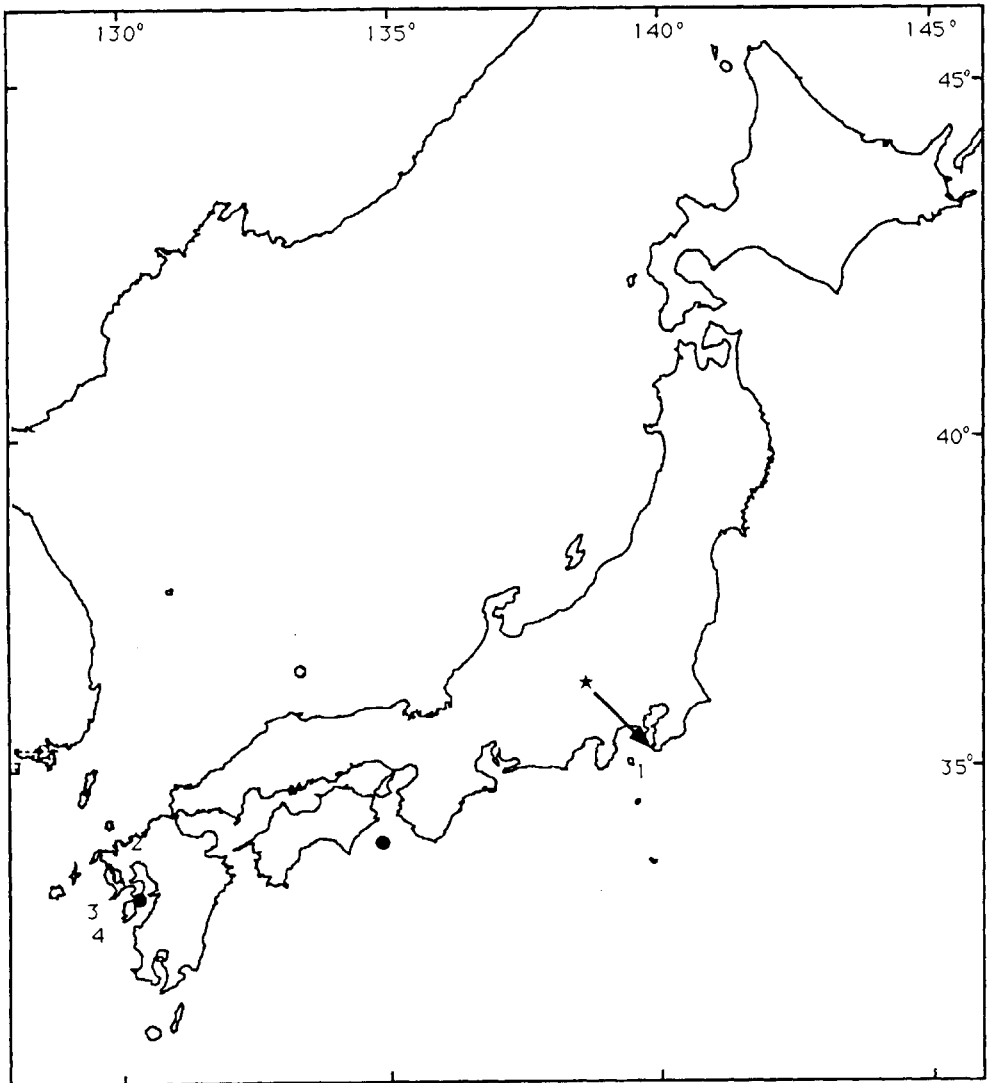


Fig. 11. Distribution of *Anapagurus japonicus* Ortmann, 1892. Star: type locality. Solid circles: based on present records. Numbers: based on previous records: 1-4-Miyake, 1978; 4-Miyake, 1961.

Sagami Bay (50-80 m). Depth range: 20-80 m.

Affinities.— As earlier noted, *A. japonicus* appears most closely related to *A. chiroacanthus*. *Anapagurus japonicus* may be distinguished from the latter by its less setose chelipeds and ambulatory legs, the unarmed, dorsolateral margin of the left cheliped, and the much longer but fewer spines of the terminal margins of the telson.

Remarks.— Ortmann (1892) recorded a male from Kadsiyama, Japan as a new variant of *Anapagurus pusillus*, and this taxon was subsequently listed as such by Alcock (1905) and Gordan (1956). Later, Miyake (1961) elevated it to specific rank, an action with which I concur.

Since S. Miyake retired from Kyushu University 18 years ago its decapod collection has been neglected. Furthermore, the collections were moved to another building, resulting in many specimens being misplaced, thus there appears to be little chance to find the specimens of *A. japonicus* listed by Miyake under ZLKU numbers (K. Baba, personal communication). Only two specimens of *A. japonicus* were available for my study, one male (ZLKU 11976) and one female (OMNH Ar 2127). The present diagnosis of the right, third pereopod, the only leg present in the male was provided by that specimen.

*Anapagurus curvidactylus* Chevreux & Bouvier, 1892  
(figs. 12, 13)

*Anapagurus curvidactylus* Chevreux & Bouvier, 1892a: 253; 1892b: 91-93, pl. II: figs. 2-8 (type locality, herein restricted by lectotype selection: "Melita" station 109, west off Gorée, Senegal, bottom of fragmented shells, 16.iii.1890); Bouvier, 1896: 152, figs. 33-35 (pictorial key); 1940: 149, 150, figs. 103, 107B (in part); Rathbun, 1900: 307 (listed); Alcock, 1905: 187 (in part); Balss, 1921: 46; Monod, 1932: 487; Forest, 1955: 128, fig. 29, pl. VI: fig. 2; 1961: 241, figs. 9, 13, 18 (in part; see remarks); 1966: 162; Gordan, 1956: 302 (listed); Cardona Bendito, 1965: 146; Anadón, 1975: 206, 214; Zariquiey Alvarez, 1968: 258; Ingle, 1985: 764 (listed).

*Anapagurus curvidactylus* var.? Forest, 1955: 129, fig. 30, pl. VI: figs. 3-5 (see remarks).

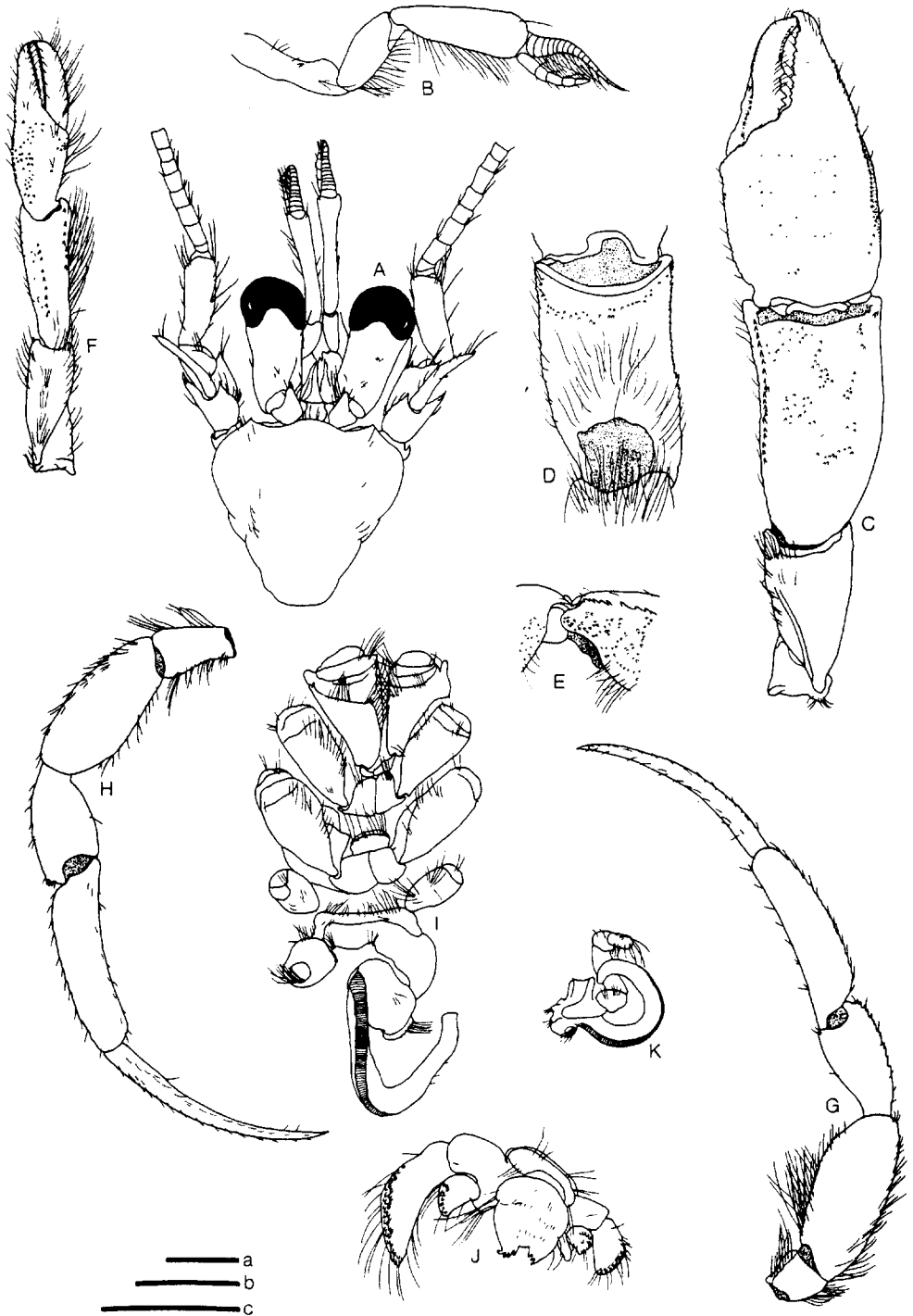
not *Anapagurus curvidactylus*; A. Milne Edwards & Bouvier, 1892: 214, 215; 1900: 225 (= *A. hyndmanni*); De Miranda y Rivera, 1933: 30, 60 (= *A. hyndmanni*) (listed).

Material.— Lectotype, herein selected: ♂ [2.0], "Melita" station 108, off Pointe Belair, Baie de Dakar, Senegal, 8 m, bottom of sand and mud, 15.iii.1890, MCZ 6578; Paralectotype: 1 ♂ [2.0], "Melita" station 109, W off Gorée, Senegal, 15 m, bottom of fragmented shells, 16.iii.1890, USNM 22921. **Eastern Atlantic: Europe:** 10 ♂ ♂ [1.8-2.1], 1 ♀ [1.9], 3 ovig. [1.2-1.6], "Flor da Ponte" station 1.634 (=F.12), 0.4 km off Los Mezos, Ría de Arosa, N.W. Spain, 18-22 m, 22.vii.1964, RMNH D 24262; 1 ♂ [2.5], "Flor da Ponte" station 1.656, 0.7 km off Punta Quilme, Isla de Arosa, Ría de Arosa, N.W. Spain, 3 m, 24.vii.1964, RMNH D 24265; **Africa:** 2 ovig. [1.0, 1.4], "Mercator", 7.4 km off Angra da Cintra, Rio de Oro, 27-36 m, 30.xii.1937, IRSNB-IG 11.553; 1 ♂ [1.2], "Mercator", along coast between Dakar and Hann, Baie de Dakar, Senegal, 13.xi.1935, IRSNB-IG 10.910; 2 ♂ ♂ [1.7, 1.8], 1 ovig. [1.3], Anse Bernard, Senegal, 8-10 m, 13.ii.1953, collector J. Forest, MNHN 488; 1 ovig. [1.5], "Atlantide" station 44, off French Guinea, 10°22'N, 16°22'W, 41 m, bottom of sand and shells, 17.xii.1945, ZMUC; 1 ovig. [1.4], "Atlantide" station 45, off French Guinea, 9°23'N, 15°07'W, 30-34 m, sandy bottom, 18.xii.1945, ZMUC; 1 ♂ [1.8], "Atlantide" station 147, off French Guinea, 9°28'N, 14°58'W, 45 m, 14.iv.1946, ZMUC; 1 ♀ [0.8], 3 ovig. [1.0-1.1], "Mercator", 3.7 km off l'Île Annobon, 16-35 m, 29.i.1938, MNHN 492; 3 ♂ ♂ [1.0-1.5], "Mercator", Baie des Eléphants, Angola, 20 m, 4.ii.1937, IRSNB-IG 11.204.

Diagnosis.— Shield slightly broader than long. Rostrum somewhat exceeding lateral projections. Lateral projections with short submarginal spine.

Ocular peduncles approximately  $\frac{3}{4}$  length of shield, with corneae slightly dilated. Ocular acicles narrowly triangular, with short, distomesial, submarginal spine. Interocular plate unarmed.

Fig. 12. *Anapagurus curvidactylus* Chevreux & Bouvier, 1892. Lectotype ♂ (SL = 2.0 mm), MCZ 6578: A, shield and cephalic appendages; B, left antennule (lateral view); C, right cheliped (dorsal view); D, carpus of same (ventral view); E, carpus of same (mesial view); F, left cheliped (dorsal view); G, right 2nd pereopod (mesial view); H, right 3rd pereopod (mesial view); I, sternum; J, extremity of abdomen, uropods and telson; K, left sexual tube (lateral view). Scales equal 1.0 mm: a: C-H, K; b: A, I; c: B, J.



Antennular peduncles exceeding distal margin of corneae approximately  $\frac{3}{4}$  length of ultimate segment. Ultimate antennular segment exceeding length of penultimate segment by approximately  $\frac{3}{5}$  own length, with 1 moderately long, dorsolateral, distal seta; ventral margin of ultimate and penultimate segments, each with row of tufts of setae, long, but not exceeding length of ventral antennular flagellum; basal segment with lateromedial spine.

Antennal peduncles overreaching distal margin of corneae approximately by  $\frac{2}{5}$  length of ultimate segment. Antennal acicles terminating in short spine, approximately reaching proximal half of corneae.

Chela of right cheliped narrow (males) or moderately broad (females). Fingers curved ventrally, strongly so in mature males. Dactyl subequal to length of palm, triangular in cross section, with dorsomedial and ventromesial, granular or spinulose ridges; all surfaces with small spinules; ventral surface with tufts of long setae. Palm approximately  $\frac{3}{5}$  length of carpus, with granular or spinulose ridge on proximal half of dorsomesial margin; dorsal surface somewhat convex, with numerous, small spinules and scattered, short setae, without ridge near dorsomesial margin proximally; dorsolateral margin with row of spinules extending onto fixed finger but becoming obsolete near claw; dorsoproximal margin with well-developed lobes, laterally and mesially, larger mesial lobe with concavity to fit the dorsomesial, distal lobe of carpus when chela is flexed; ventroproximal margin with skewed, subquadrate sinus near ventromesial margin. Carpus exceeding merus by approximately  $\frac{2}{5}$  own length, shorter in females; dorsomesial margin with irregular row of closely spaced, short spines; dorsomesial, distal angle produced into concave, subcircular structure; dorso-distal margin with weak subcircular projection adjacent to dorsomesial, distal angle; mesial face somewhat compressed; dorsolateral face rounded, slightly inflated, without delimiting, dorsolateral margins; dorsolateral, distal angle produced into small, subcircular lobe; ventromesial margin subcircular in mesial view; moderately long, ventral length between shallow, subcircular, ventrodistal and ventroproximal margins; mesial and dorsolateral faces each with small spinules and scattered short setae; ventral surface with spinules and scattered, stiff, short (females) or long (males) setae. Dorsal margin of merus with row of moderately long setae and short, distal spine; ventromesial margin with short, distal spine and slightly developed protuberance (males); ventrolateral margin with 4 to 6 strong spines; ventral surface with spinules and scattered setae, short (females) or long (males). Ischium with 1 spinule on ventrolateral margin partly covered by tufts of setae, short (females) or long (males); ventromesial margins minutely serrate. Coxae of chelipeds with 1, occasionally 2, short, ventrolateral distal spines.

Dactyl of left cheliped smooth but with tufts of long, stiff setae. Dorsomesial margin of carpus with row of 8 to 10 short, closely spaced spines on distal half; dorsolateral margin with row of 8 to 10 short, closely spaced spines becoming obsolete distally.

Ambulatory legs with dactyls exceeding propodi by approximately  $\frac{1}{4}$  own length, with lateral and mesial faces each with row of widely spaced, short setae near dorsal and ventral margins, dorsomesial setae stiffer. Propodi exceeding carpi by nearly  $\frac{1}{3}$  own length; dorsal surfaces serrate, each with row of tufts of widely spaced short, stiff setae; lateral and mesial faces each with row of widely spaced, short setae near dorsal and ventral margins; ventromesial distal angle unarmed but with 1 short,

simple seta. Carpi approximately  $\frac{2}{3}$  length of meri; dorsal surfaces with row of tufts of short, stiff setae and short spines increasing in size distally (2nd) or 1 to 3 distal spines (3rd). Dorsal surfaces of meri each with row of tufts of moderately long setae; ventral margins with row of spinules and tufts of long setae (2nd) or unarmed but with row of moderately long setae (3rd). Lobes of sternite of 2nd pereopods unarmed, distally rounded. Anterior lobe of sternite of 3rd pereopods subrectangular; anterior margin with tufts of moderately long setae.

Males with very long, left sexual tube, strongly recurved to level dorsodistal margin of branchiostegite; coxa of right 5th pereopod with gonopore on distoventral surface, partly covered by tufts of moderately long setae; three uniramous pleopods. Right distal protopodal lobe equaling length of uropodal endopod.

Telson with posterior, asymmetrical lobes separated by wide, shallow cleft; terminal margins each with 3 or 4 short spines; lateral margins unarmed but with tufts of moderately long setae.

Colour.— "L'animal est blanc avec une bande brun jaunatre a la base des doigts des pattes ambulateoires, ainsi qu'a la base et au sommet du propode des memes pattes". (Chevreux & Bouvier, 1892).

Related organisms.— In the present collections, specimens of *A. curvidactylus* have been found inhabiting the following gastropod shells: *Hinia reticulata* (5 specimens, RMNH D 24262); and *Turritella biplicata* (1 specimen, MNHN 492).

One ovigerous female of *A. curvidactylus* collected at station 44 by the "Atlantide" (ZMUC) was found in a gastropod shell so encrusted by a colonial bryozoan, that it extend past the shell aperture in the form of a helicospiral coil (Taylor & Cook, 1981). According to Taylor *et al.* (1989), this association between hermit crab and bryozoan is probably mutualistic.

On three males of *A. curvidactylus* collected in Ría de Arosa, Spain (RMNH D 24262), there were folliculinid protozoans type 1 (see section on related organisms for *A. hyndmanni*); tests were cemented dorsally to the abdomen, telson and protopod of the right uropodal exopod. Colonial hydrozoans were found dorsally on the carpus of the right cheliped on one of these specimens. No external changes caused were observed that could be attributed to these symbionts. The above are the first records of folliculinids and hydrozoans associated with *A. curvidactylus*.

Distribution.— Eastern Atlantic: from Ría de Arosa, northwest Spain to Baie des Eléphants, Angola. Depth range: 0-45 m.

Affinities.— As previously stated, *A. curvidactylus* is most closely related to *A. hyndmanni*. The former species can be distinguished by the much shorter ultimate antennular segment bearing ventral setae shorter than the ventral antennular flagellum, the shorter antennal acicles, the absence of longitudinal sulci on the lateral and mesial faces of the ambulatory dactyls, and the much longer, left sexual tube.

Remarks.— In a preliminary note on the pagurids collected by the "Melita" off the Canary Islands and Senegal, Chevreux & Bouvier (1892a) briefly described *A. curvidactylus*. Subsequently (1892b), they more completely described and illustrated this taxon. A. Milne Edwards & Bouvier (1892, 1900) identified a male specimen from the "Travailleur" collections off Barquero, Bay of Viscay, Spain, as *A. curvidactylus*; however my subsequent examination of this specimen has shown it to represent *A. hyndmanni*. De Miranda y Rivera (1933) just listed A. Milne Edwards & Bouvier's

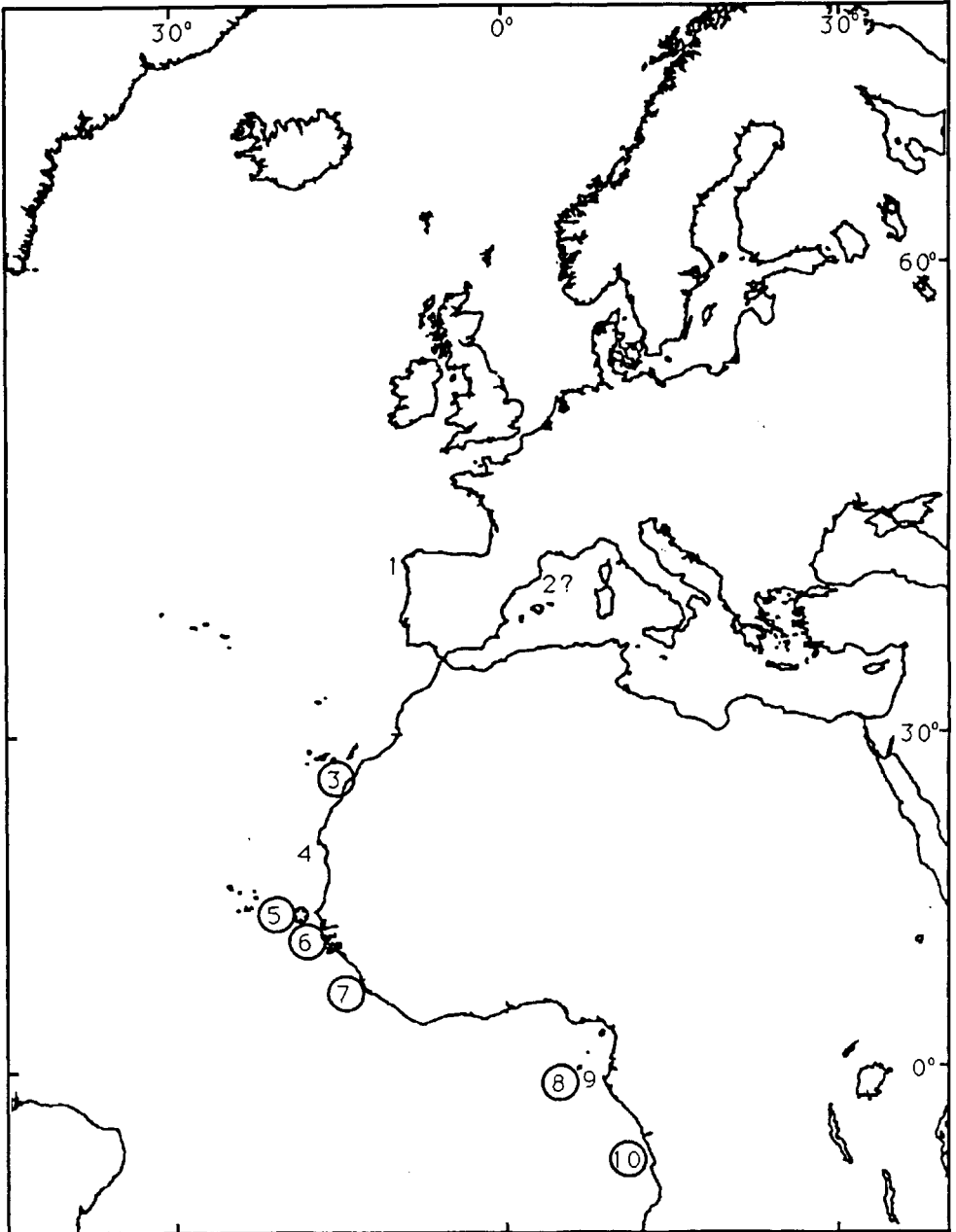


Fig. 13. Distribution of *Anapagurus curvidactylus* Chevreux & Bouvier, 1892. Circled star: type locality, material examined. Solid circles: based on present records. Numbers: based on previous records (circled numbers: material examined): 1-Cardona Bendito, 1965; 2?-Zariquiey Alvarez, 1968 (questionable material); 3, 5, 8, 10-Forest, 1955; 6-Chevreux & Bouvier, 1892a, 1892b, 7-Forest, 1961; 9-Forest, 1966.

(1892) reference of *A. curvidactylus* from the Cantabric region, which indeed refers to *A. hyndmanni*. References by other authors (Alcock, 1905; Bouvier, 1940) who cited *A. Milne Edwards & Bouvier's* work (1892, 1900) are listed as "in part" in the synonymy. I have also had the opportunity to examine the four females collected by the "Mercator" along the Island of Annobon that Forest (1955) doubtfully assigned to a variety of *A. curvidactylus*, and have confirmed that they indeed do belong to Chevreux & Bouvier's taxon. I have additionally examined the specimens collected by the "Atlantide" along the coasts of tropical west Africa that Forest (1961) doubtfully identified as *A. curvidactylus*, and have found that they are conspecific with *A. wolffi*.

*Anapagurus bicorniger* A. Milne Edwards & Bouvier, 1892  
(figs. 14, 15)

*Anapagurus bicorniger* A. Milne Edwards & Bouvier, 1892: 215, 216 (type locality: Golfo de Cádiz, "Talisman" station 2, 100 m); 1898: 1247 (listed); 1899: 66; 1900: 220-223, pl. XXV: figs. 14-22; Bouvier, 1896: 152, fig. 30; 1940: 152, figs. 106, 107 E; Alcock, 1905: 187 (listed); Balss, 1926: 375-377, fig. 1; De Miranda y Rivera, 1933: 30, 60 (listed); Fenizia, 1937: 33, 34 (in part; see remarks), fig. 24, not pp. 35, 36, figs. 25, 26 (= *A. petiti*); Gordan, 1956: 302 (listed); Forest, 1958: 100; Holthuis & Gottlieb, 1958: 73; Pike & Williamson, 1960: 528-531, fig. 9 (larvae); Dechancé & Forest, 1962: 294-296, figs. 1, 3-5, 9, 11 (in part; see remarks); Zariquiey Alvarez, 1968: 259 (in part; see remarks); Gilat, 1969: 16, 54; Neves, 1977: 182, 183; Calafiore, 1981: 20 (larvae); Kocatas, 1981: 162; García Raso, 1982: 503, 504, fig. 4; Ingle, 1985: 764 (listed).

Not *Anapagurus bicorniger*; Zariquiey Alvarez, 1946: 122, 123 (= *A. petiti*); 1955: 402 (= *A. petiti*).

Material.— Syntypes: "Talisman" station 2, Golfo de Cádiz, South off Cabo de São Vicente, 36°53'N, 10°52'W, 99 m, bottom of silt and shells, 6.vi.1883: 2 ♂♂ [5.8, 6.0], 1 ovig. [2.0] (USNM 22920); 2 ♂♂ [1.2, 2.1], 2 ovig. [2.2] (MCZ 6577); 1 ♀ [1.8], 1 ovig. [2.1] (RMNH D 1658); 1 ♂ [2.4], 1 ♀ [2.4], 1 ovig. [2.0] (ZMUC). **Mediterranean Sea: Off Balearic Islands:** 1 ovig. [1.3], "AAK" station 1364, 38°43'N, 2°30.8'E, 125 m, bottom of *Lithothamnium* with sand and clay, 27.iv.1980, collector N.A. Valovaya, MMSU. **Golfo de Valencia:** 1 ♂ [1.5], 1 ♀ [1.4], 1 ovig. [1.9], "AAK" station 1247, 40°26.2'N, 1°09.2'E, 90 m, bottom of clay and sand, 9.iv.1978, collectors V.V. Murina & V.D. Tchukhtchin, MMSU; 1 ovig. [1.4], "AAK" station 1251, 40°17.0'N, 0° 46.9'E, 77 m, bottom of sand and clay, 15.iv.1978, collectors V. V. Murina & V.D. Tchukhtchin, MMSU; 1 ovig. [1.8], "AAK" station 1252, 40°11.6'N, 0°55.4'E, 90 m, bottom of sand and clay, 15.iv.1978, collector V.D. Tchukhtchin, MMSU; **Golfo de Rosas:** 1 ovig. [2.2], South of Cabo de Creus, 73-91 m, 3.ix.1945, collector R. Zariquiey Alvarez, MNHN 469; **Ligurian Sea:** 1 ovig. [2.1], "Princess Alice" station 633, 43°44'10"N, 5°06'50"E, 69 m, 12.v.1896, MOM 38-0353; 1 ♂ [1.9], 2 ovig. [1.8, 2.2], off Roquebrune, 72-80 m, 30.vii.1963, RMNH D 19707; 1 ♂ [2.2], off Portofino, 1914, collector L. Nick, SMF 8764. **Tyrrhenian Sea:** 1 ♂ [2.1], 2 ♀♀ [1.7, 2.0], "Dana" station 4088, off Castellamare, 64 m, 26.v.1930, collector R. Spack, ZMUC. **Adriatic Sea:** 4 ♂♂ [2.1-2.5], 3 ♀♀ [1.9-2.2] off Rodi Garganico, 20 m, 8.viii.1978, collector C. Frogliia, IRPEM-D 589; 1 ♂ [2.5], 1 ovig. [2.2], 42°25'N, 14°30'E, 60-65 m, 18.viii.1978, collector C. Frogliia, IRPEM-D598; 2 ♂♂ [1.8, 2.0], 3 ovig. [2.1-2.4], 43°30'N, 13°48'E, 20 m, 18.x.1972, collector C. Frogliia, IRPEM-D382; 2 ♂♂ [2.7], 1 ovig. [2.2], off Ancona, 13 m, v.1982, collector C. Frogliia, MSNM 2384; 1 ♂ [2.6], 43°38.1'N, 13°26.4'E, 5 m, 12.iv.1973, IRPEM; 1 ♂ [2.7], 12 miles north of Ancona, viii.1987, collector C. Frogliia, UMMML; 10 ♂♂ [2.2-3.1], 9 ovig. [2.5-2.8], off Senigallia, 14 m, 2.ix.1986, collector C. Frogliia, IRPEM; 1 ♂ [2.5], 1 ovig. [2.8], off Senigallia, 13 m, 30.ix.1975, collector C. Frogliia, CF470; 5 ♂♂ [2.2-2.7], 1 ♀ [2.6], 2 ovig. [2.2, 2.7], between Esino and Misa, 13 m, 29.vii.1976, collector C. Frogliia, IRPEM-D497; 2 ♂♂ [2.6], 2 ovig. [2.2, 2.3], 43°42'N, 13°30'E, 21 m, 2.iv.1973, collector C. Frogliia, IRPEM-D367; 1 ♂ [2.7], 43°47'N, 13°21'E, 20 m, 24.x.1972, collector C. Frogliia, IRPEM-D368; 1 ♂ [2.6], 2 ♀♀ [2.6, 2.7], 2 ovig. [2.4, 2.9], 43°47'N, 13°21'E, 20 m, 24.x.1972, collector C. Frogliia, IRPEM-D383; 6 ♂♂ [2.3-3.0], 2 ♀♀ [2.6], 4 ovig. [2.4-2.8], 43°47'N, 13°23'E, 23 m, 6.xi.1973, collector C. Frogliia, CF 162; 4 ♂♂ [2.8-3.1], 2 ovig. [2.5, 2.6], between

Fano and Senigallia, 22-25 m, 11.viii.1975, collector C. Froglija, CF 474; 3 ♂♂ [2.6-3.0], from 43°56'N, 13°15'E to 43°52.6'N, 13°17.7'E, 34-36 m, 11.viii.1975, collector C. Froglija, IRPEM-D394; 6 ♂♂ [2.6-2.7], 1 ovig. [2.5], 43°54'N, 13°26'E, 55 m, 7.v.1973, collector C. Froglija, IRPEM-D366; 1 ♂ [2.2], 1 ovig. [2.7], off Rovinj, 32 m, 10.ix.1985, collector Exk. Uni Frankfurt, SMF 13973; 1 ovig. [2.0], off Split, 30-35 m, bottom of sand, 5.iv.1932, NHRM 13953; 1 ♂ [1.6], off Split, 40 m, bottom of bryozoans, RMNH D 16162. Aegean Sea: 1 ovig. [1.5], off Izmir, RMNH D 20709. Off Israel: 1 ♂ [1.7], 4 ovig. [1.4-2.0], off Ashdod, 50 m, RMNH D; 2 ♂♂ [1.3, 1.4], 1 ovig. [1.7], off Palmahim, RMNH D; 13 ♂♂ [1.2-2.1], 2 ♀♀ [1.5, 1.8], 5 ovig. [1.6-1.9], 31°55'N, 34°33'E, 80 m, 24-26.i.1977, TAU-NS-17125 (AR).

Diagnosis.— Shield broader than long. Rostrum slightly exceeded by lateral projections. Lateral projections with short submarginal spine.

Ocular peduncles approximately  $\frac{3}{4}$  length of shield, with corneae moderately dilated. Ocular acicles narrowly subtriangular, with short submarginal spine. Interocular plate with 2 chitinous spines usually not reaching proximal half of ocular acicles.

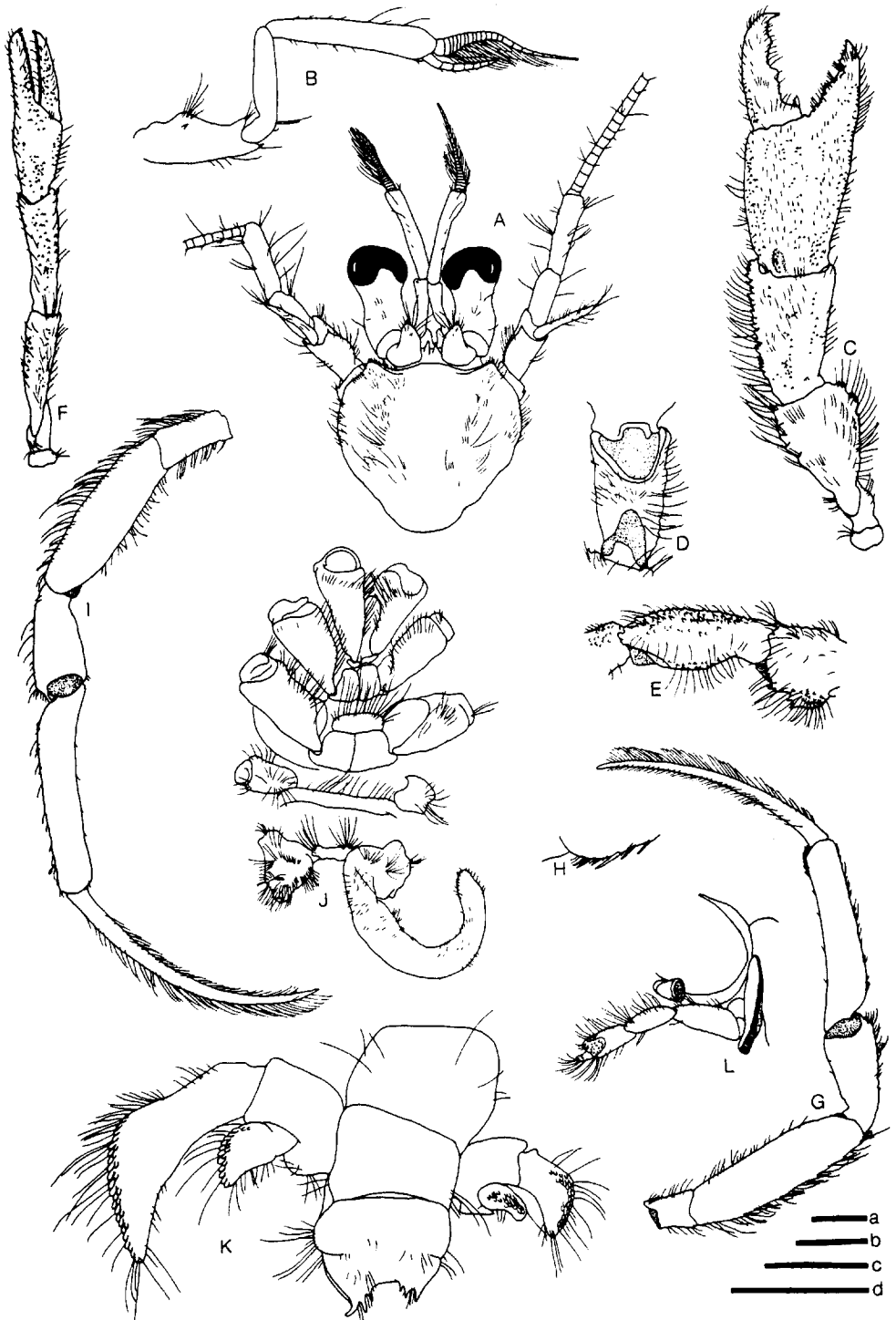
Antennular peduncles exceeding distal margin of corneae by approximately  $\frac{2}{3}$  length of ultimate segment. Ultimate segment exceeding length of penultimate segment by approximately  $\frac{1}{2}$  own length, with dorsolateral row of short setae and 2 moderately long setae on distal half, ventral margin with row of very short setae; basal segment with lateromedial, laterodistal and dorsodistal spines.

Antennal peduncles exceeding distal margin of corneae by approximately  $\frac{1}{4}$  length of ultimate segment. Antennal acicles with distal short spine, not reaching corneae distally.

Right cheliped with moderately narrow chela; in mature males prominent hiatus between dactyl and fixed finger distally. Dactyl approximately  $\frac{3}{4}$  length of palm, with granules more numerous on mesial surface and near dorsomesial margin and tufts of moderately long setae. Palm slightly longer than carpus; dorsomesial margin with numerous spinules and moderately long setae and with slightly developed ridge in proximal half; dorsal surface somewhat convex, with scattered spinules and tufts of short setae, and short, low, spinulose ridge near dorsomesial margin proximally; dorsolateral margin with row of spinules extending onto fixed finger and becoming obsolete near claw; dorsoproximal margin with weakly developed mesial and lateral lobes; ventroproximal margin with median, subquadrate sinus. Carpus approximately equal to length of merus; dorsomesial margin with irregular row of numerous short spines; dorsomesial distal angle produced into subrectangular structure with spinulose margins; dorsodistal margin with weak, triangular projection adjacent to dorsomesial distal angle; dorsolateral margin with row of granules or spinules; lateral face unarmed; ventromesial margin subcircular in mesial view; ventral surface granular and with tufts of long setae; very short ventral length between deep, subtriangular, ventrodistal margin and deep, subcircular, ventroproximal mar-

Fig. 14. *Anapagurus bicorniger* A. Milne Edwards & Bouvier, 1892. A-K ♂ (SL = 3.0 mm), off Senigallia, Adriatic Sea, IRPEM: A, shield and cephalic appendages; B, right antennule (lateral view); C, right cheliped (dorsal view); D, carpus of same (ventral view); E, carpus of same (mesial view); F, left cheliped (dorsal view); G, right 2nd pereopod (mesial view); H, ventromesial distal angle of propodus of same; I, right 3rd pereopod (mesial view); J, sternum; K, extremity of abdomen, uropods and telson; L, syntype ♂ (SL = 2.1 mm), MCZ 6577: left sexual tube (lateral view). Scales equal 1.0 mm: a: G, I; b: A, C-F, J, L; c: B; d: H, K.





gin. Ventromesial margin of merus with prominent spinose or spinulose protuberance in males; dorsal margin unarmed distally. Coxae of chelipeds with ventrolateral, distal angle unarmed.

Dactyl of left cheliped granulose or spinulose and with tufts of moderately long setae. Dorsomesial margin of carpus with row of closely spaced spines on distal half, increasing in size distally; dorsolateral margin with 1 strong spine on proximal half.

Dactyls of ambulatory legs exceeding propodi by approximately  $\frac{1}{4}$  own length, dorsomesial and ventromesial margins each with closely spaced, moderately long setae. Propodi exceeding carpi  $\frac{1}{2}$  to  $\frac{2}{3}$  own length; ventromesial distal angle in adult males with 4-8 corneous spines of various sizes (2nd) or unarmed (3rd); in females, both (2nd and 3rd) unarmed. Carpi  $\frac{1}{2}$  to  $\frac{2}{3}$  length of meri; dorsal margins each with 1 proximal and 1 distal spine; meri with 2, or occasionally 3, widely spaced spinules on dorsal margin and 1 spinule on distal third ventrally. Lobes of sternite of 2nd pereopods unarmed, slightly expanded laterodistally. Anterior lobe of sternite of 3rd pereopods subrectangular.

Males with moderately long, left sexual tube and conical, short, backwardly directed, right sexual tube. Pleopod 3 unequally biramous, pleopods 4 and 5 uniramous. Distal protopodal lobe of right uropod less than  $\frac{1}{2}$  length of endopod.

Telson with posterior asymmetrical lobes, separated by wide, median cleft; terminal margins each with 3 strong spines.

Colour.— A. Milne-Edwards & Bouvier (1892) and Bouvier (1940) described the colour as generally whitish.

Related organisms.— A. Milne-Edwards & Bouvier (1900: 222) reported turritelids as the gastropods shells inhabited by some of the syntypes of *A. bicorniger*. In the present collections, specimens of *A. bicorniger* have been found in the following shells: *Turritella biplicata* (1 specimen, MMSU-AAK-1247), and *Amyclina* sp. (6 specimens, RMNH D; and 6 specimens, TAU-NS-17125-AR).

One of the *Amyclina* sp. inhabited by a male *A. bicorniger* (RMNH) was completely covered by colonial hydroids.

One male of *A. bicorniger* (IRPEM-D394) was parasitized by one *Peltogaster paguri*. No external effects of the parasite were observed. This represents the first record of a rhizocephalan in *A. bicorniger*.

Folliculinid protozoans type 1 (see section on related organisms for *A. hyndmani*) were found on 26 specimens of *A. bicorniger* collected at different stations in the Adriatic Sea (MCSN 2384; IRPEM D368, D382, D383, D394, D497, and D589; CF 162, 470 and 474), and on one specimen from the Gulf of Rosas (MNHN-469). The folliculinids usually ranged in number from 1 to 12, occasionally 39 and 81, specimens per host; most tests are cemented dorsally to the posterior carapace, abdomen, and along the groove outlining the last abdominal segment. These are the first records of folliculinids associated with *A. bicorniger*.

Distribution.— Northeastern Atlantic: from off the Portuguese coast of Guia (Neves, 1977) to the Golfo de Cádiz. Mediterranean Sea: from the Golfo de Valencia, Spain, to off the coast of Palmahim, Israel. Larvae of *A. bicorniger* were studied in the Gulf of Naples (Pike & Williamson, 1960) and in the Strait of Messina (Calafiore, 1981). Depth range: 2-200 m.

Affinities.— The interocular-plate spines immediately distinguish *A. bicorniger*

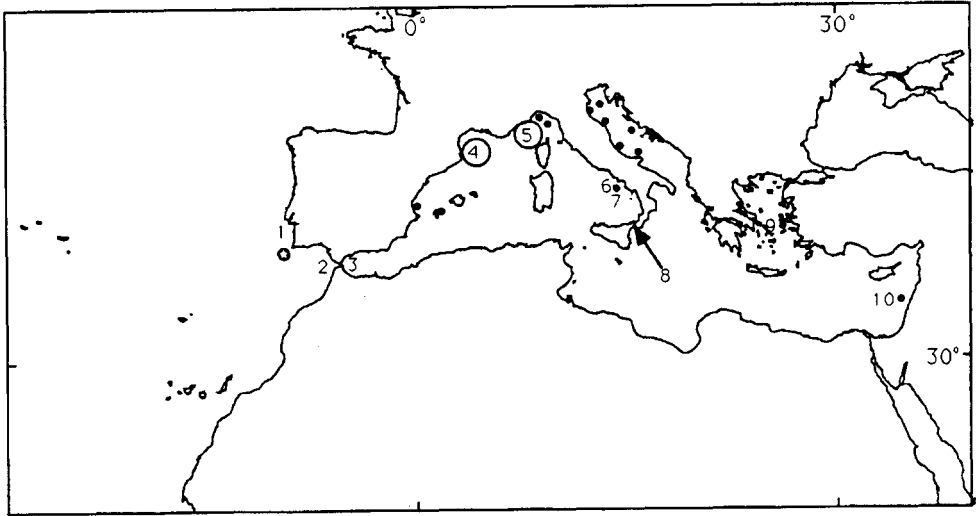


Fig. 15. Distribution of *Anapagurus bicorniger* A. Milne Edwards & Bouvier, 1892. Circled star: type locality, material examined. Solid circles: based on present records. Numbers: based on previous records (circled numbers, material examined). 1-Neves, 1977; 2, 3-García Raso, 1982; 4-Dechancé & Forest, 1962; 5-A. Milne Edwards & Bouvier, 1899; 6-Fenizia, 1937; 7-Pike & Williamson, 1960; 8-Calafiore, 1981; 9-Kocatas, 1981; 10-Holthuis & Gottlieb, 1958.

and *A. petiti* from other congeners. *Anapagurus bicorniger* can be distinguished from *A. petiti* by the much narrower ocular acicles, the shorter interocular-plate spines, the much longer and armed antennal acicles, the more numerous but smaller carpal spines of the right cheliped, and the more numerous and longer ventral setae of the dactyls of the ambulatory legs.

Remarks.— A. Milne Edwards & Bouvier (1892) briefly described *A. bicorniger* from specimens collected in the Golfo de Cádiz. These authors simply listed *A. bicorniger* in their 1898 work and subsequently (1899) reported its occurrence in the Mediterranean for the first time. A. Milne Edwards & Bouvier (1900) provided illustrations and a more detailed specific description based on specimens collected off Monaco. Since its original description, *A. bicorniger* has been easily distinguished from the other congeners by the two interocular-plate, chitinous spines. It was not until 1962 that Dechancé & Forest realized that Balss (1926) and Fenizia (1937) had incorrectly identified specimens as *A. bicorniger* that actually represented their new species *A. petiti*. My reexamination leads me to believe that while Fenizia (1937) did fail to recognize the differences between some of his specimens and *A. bicorniger*, Balss (1926) was correct in his identification. There is an overlap in the number of the propodal ventromesial distal spines on the 2nd pereopods of adult males in *A. bicorniger* (4-8 spines) and *A. petiti* (6-10 spines). Furthermore in both taxa these propodal, ventromesial, distal spines are interspersed with spine-like setae making the counting difficult. The carpal armature of the 2nd pereopods is also variable in both taxa. The present collections have shown that the ventromesial, spinose, meral protuberance of the right cheliped in adult males, which has been used to separate *A. bicorni-*

*ger* and *A. petiti*, is also present in the latter taxon. Although Dechancé & Forest (1962) and Zariquiey Alvarez (1968) correctly included in *A. petiti* those specimens cited by Zariquiey Alvarez (1946 and 1955) as *A. bicorniger*, they overlooked the structural overlap in the 2nd pereopods in both species and perhaps were mistaken in citing Balss (1926) as "in part" (pro parte) in their synonymy of *A. Milne Edwards & Bouvier's* taxon.

*Anapagurus longispina* A. Milne Edwards & Bouvier, 1900  
(figs. 16, 17)

*Anapagurus laevis*; A. Milne Edwards & Bouvier, 1892: 214 (in part; see remarks); 1894: 72 (in part; see remarks); 1900: 217 (in part; see remarks), not pl. XXVIII: figs. 9, 10; Holthuis & Gottlieb 1958: 72 (in part; see remarks); Türkay, 1976: 36 (in part; see remarks).

*Anapagurus laevis* var. *longispina* A. Milne Edwards & Bouvier, 1900: 219 (type locality: "Talisman" station 2, off Cabo de São Vicente, 39°53'N, 10°52'W, Golfo de Cádiz, SW Portugal, 99 m, bottom of silt and shells); Bouvier, 1905: 1 (listed); 1922: 31; Gordan, 1956: 303 (listed).

*Anapagurus longispina*; Forest, 1965: 359, figs. 19, 21, 22 (not citation of figures 12 and 13 in synonymy of *A. Milne Edwards & Bouvier 1900's* work)(see remarks); Zariquiey Alvarez, 1968: 257 (not citation of figures 12 and 13 in synonymy of *A. Milne Edwards & Bouvier 1900's* work)(see remarks); Kocatas, 1981: 162 (not examined); Ingle, 1985: 764 (listed).

Material.— Holotype: ♂, "Talisman" station 2, off Cabo de São Vicente, 39°53'N, 10°52'W, Golfo de Cádiz, SW Portugal, 99 m, bottom of silt and shells, 6.vi.1883, unknown deposition; not examined. **Northeastern Atlantic:** 1 ovig. [1.9], "Josephine" Expedition station c72, off the Azores, 36°48.5'N, 14°12.2'W, 296.3 m, 1869, NHRM 6999; 1 ♂ [1.4], "Hirondelle" station 226, Strait of Pico-Fayal, Azores, 130 m, 14.viii.1888, MOM 380157; 1 ovig. [1.5], "Meteor" station 9c90, off Portuguese coast, 37°14.7'N, 9°15.5'W, 114-117 m, 22.vi.1967, collector H. Thiel, SMF 21926; 1 ♂ [2.0], "Meteor" station 19-210, Josephine Seamount, 36°41'N, 14°16.18'W, 223-237 m, 11.iii.1970, collector H. Thiel, SMF 5986; 1 ♂ [2.6], "Meteor" station 9c-123a, Josephine Seamount, 36°42.3'N, 14°15.2'W, 210-231 m, 2.vii.1967, collector H. Thiel, SMF 5987; 1 ♂ [2.3], "Meteor" station 9c-130, Josephine Seamount, 36°41.4'N, 14°14.8'W, 216-225 m, 3.vii.1967, collector H. Thiel, SMF 5988; 2 ♂ ♂ [2.0, 2.1] (USNM 22922) and 1 ♂ [2.0] (MCZ 6580), "Talisman" station 2, off Cabo de São Vicente, 39°53'N, 10°52'W, Golfo de Cádiz, 99 m, bottom of silt and shells, 6.vi.1883; 1 ♂ [1.5], "Princesse Alice" station 2034, Banc Seine, 33°47', 14°21'W, 185 m, 26.vii.1905, MOM 380921. **Mediterranean Sea:** 1 ♂ [1.7], "AAK" station 1192-129, 40°03.0'N, 0°56.1'E, 105 m, bottom of sand and fragmented shells, 2.vi.1974, collector V.V. Murina, MMSU; 1 ovig. [1.9], "AAK" station 1261, 37°26.8'N, 12°11.6'E, 57 m, bottom of sandy clay, collector V.V. Murina, MMSU; 1 ♂ [2.8], 2 ovig. [2.4, 2.5], "AAK" station 1296, 37°30.7'N, 12°06.5'E, 86 m, sandy bottom, 10.ix.1979, collectors V.V. Murina & V.D. Tchukhtchin, MMSU; 4 ♂ ♂ [1.9-2.5], 1 ♀ [2.7], "AAK" station 1305, 37°31.9'N, 11°49.9'E, 70 m, bottom of clayed sand, 14.ix.1979, collectors V.V. Murina & V.D. Tchukhtchin, MMSU; 1 ♂ [1.9], "AAK" station 1308, 37°08.9'N, 12°05.2'E, 65 m, bottom of sand and fragments of *Lithothamnium*, 15.ix.1979, collector V.V. Murina, MMSU; 1 ♂ [2.4], "AAK" station 1398, 37°23.6'N, 12°16.5'E, 70 m, sandy bottom, 7.ix.1980, collectors V.V. Murina & V.D. Tchukhtchin, MMSU; 1 ovig. [2.0], "AAK" station 1265, 35°27.0'N, 11°39.3'E, 70 m, bottom of clayed sand, 26.iv.78 collector V.V. Murina, MMSU; 6 ♂ ♂ [1.6-2.4], 3 ♀ ♀ [1.9-2.4], "AAK" station 1392, 35°7'N, 12°01.2'E, 72 m, bottom of sand and *Lithothamnium*, 3.ix.1980, collectors V.V. Murina & V.D. Tchukhtchin, MMSU; 2 ♂ ♂ [1.6-2.0], AAK 1273-82, 35°56.3'N, 15°00.0'E, 91 m, 30.iv.1978, sandy bottom with fragments of shells and *Lithothamnium*, collector V.V. Murina, MMSU; 4 ♂ ♂ [1.9-2.4], 1 ♀ [1.8], "AAK" station 1286, 35°49.0'N, 14°53.8'E, 91 m, sandy bottom with fragmented shells, 1.ix.1979, collector V.V. Murina; 5 ♂ ♂ [1.9-2.2], 3 ♀ ♀ [1.6-2.1], "AAK" station 1288, 35°38.8'N, 15°01.7'E, 97 m, bottom of clayed sand, 2.ix.1979, collector V.V. Murina, MMSU; 2 ♂ ♂ [1.6, 1.9], 31°32'N, 32°56'E, 73.2 m, bottom of sand and mud, 1.xi.1975, collector C. Lewinsohn, TAU 15905; 1 ♂ [1.2], sample 201, station 6, Haifa Bay, Israel, 70 m, 16.v.1955, collector E. Gottlieb, RMNH D 13728; 1 ovig. [1.4], sample 191, station 6→

5 (6), Haifa Bay, Israel, 79 m, 5.iv.1955, collector E. Gottlieb, RMNH D 13736; 1 ovig. [1.3], sample 695, off Atlit, Israel, 90 m, 9.ix.1948, collector A. Wirzubski, RMNH D 13744. Southeastern Atlantic: 1 ovig. [2.1], off Porto Alexandre, Angola, 109.7 m, 11.viii.1912, collector Skoog, NHMG 14062.

**Diagnosis.**— Shield slightly broader than long. Rostrum approximately equaling lateral projections. Lateral projections with short submarginal spine.

Ocular peduncles approximately  $\frac{3}{4}$  length of shield; with corneae moderately to strongly dilated. Ocular acicles narrowly triangular, with long marginal spine. Interocular plate unarmed.

Antennular peduncles exceeding distal margin of corneae approximately  $\frac{2}{3}$  length of ultimate segment. Ultimate segment exceeding length of penultimate segment by approximately  $\frac{2}{5}$  own length, with dorsolateral, dorsomesial and ventral margins, each with row of moderately long setae; dorsolateral distal angle with tuft of setae composed on 1 long seta and 2 or 3 moderately long setae decreasing in length laterally; basal segment unarmed but with tuft of long setae.

Antennal peduncles exceeding distal margin of corneae by approximately  $\frac{1}{2}$  length of ultimate segment. Antennal acicles terminating in moderately long spine, usually reaching corneae distally.

Right cheliped with narrow chela. Dactyl approximately  $\frac{3}{5}$  length of palm, with tufts of moderately long setae and spinules more numerous on mesial surface and near dorsomesial margin. Palm slightly shorter than carpus, with somewhat developed spinulose ridge on dorsomesial margin proximally; dorsal surface moderately convex, spinulose, with scattered, short setae, with low, broad spinulose ridge near dorsomesial margin proximally; dorsolateral margin with row of closely spaced spinules extending and becoming more numerous on fixed finger but becoming obsolete near claw; dorsoproximal margin with weakly developed lateral lobe and almost vestigial mesial lobe; ventroproximal margin with median, skewed subrectangular sinus. Carpus exceeding merus approximately by  $\frac{1}{3}$  own length; dorsomesial margin with row of 4 or 5 acute spines interspersed with spinules and moderately long setae; dorsomesial distal angle produced into moderately large, concave subquadrate structure; dorsodistal margin with weak, triangular projection adjacent to dorsomesial distal angle; dorsal surface depressed, spinulose or granular; dorsolateral margin with row of 3 or 4 moderately long spines; dorsolateral distal angle produced into small lobe; lateral face moderately convex, with numerous spinules and tufts of short setae; mesial face slightly compressed with scattered granules and moderately long setae; ventromesial margin subcircular in mesial view; ventral surface spinulose and with tufts of long, stiff setae; moderately short ventral length between deep, subtriangular ventrodistal margin and deep, subcircular ventroproximal margin. Dorsal margin of merus with acute distal spine; ventromesial margin with spinules and acute distal spine; ventrolateral margin with 3 or 4 acute spines; ventral surface spinulose, with tufts of long, stiff setae. Ischium with 1 spinule on ventrolateral margin; ventromesial margin minutely serrate. Coxae of chelipeds with ventrolateral distal angle unarmed.

Dactyl of left cheliped smooth but with tufts of moderately long setae. Dorsomesial margin of carpus with 3 or 4 strong, widely spaced spines; dorsolateral margin with row of 5 or 6 strong, closely spaced spines.

Ambulatory legs with dactyls exceeding propodi by approximately  $\frac{1}{5}$  own length, with dorsomesial row of moderately long setae increasing in length distally,

and mediomesial and ventromesial rows of short setae; lateral faces each with row of widely spaced, short setae near dorsal and ventral margins. Propodi approximately twice length of carpi; dorsal surfaces each serrate and with row of short setae; mesial and lateral faces glabrous; ventromesial margin with widely spaced, very short setae; ventromesial distal angle with corneous spines decreasing in size distally, 4 to 6 long (2nd, males), 3 to 5 short (2nd, females), 1 very short (3rd, both sexes). Carpi  $\frac{2}{3}$  to  $\frac{2}{5}$  length of meri; dorsal surfaces serrate, each with 1 proximal and 1 distal spine and row of short setae. Dorsal margin of meri with 2 spinules, 1 on proximal half and 1 on distal third (2nd); ventral margins serrate, with 1 spinule on distal third (2nd) or unarmed (3rd); both margins with rows of short setae. Lobes of sternite of 2nd pereopods unarmed, distally rounded. Anterior lobe of sternite of 3rd pereopods subrectangular; anterior margin with tufts of long setae.

Males with left sexual tube directed diagonally toward exterior, and then upwardly recurved to level of dorsodistal margin of branchiostegite. Coxa of 5th right pereopod with short sexual tube backwardly directed, partly covered with tufts of moderately long setae. Pleopods 3 and 4 unequally biramous, pleopod 5 uniramous. Distal protopodal lobe of right uropod approximately  $\frac{1}{2}$  length of endopod.

Telson with strongly asymmetrical posterior lobes separated by moderately broad, shallow cleft; terminal margins each with 3 or 4 short spines; lateral margins unarmed but with tufts of moderately long setae.

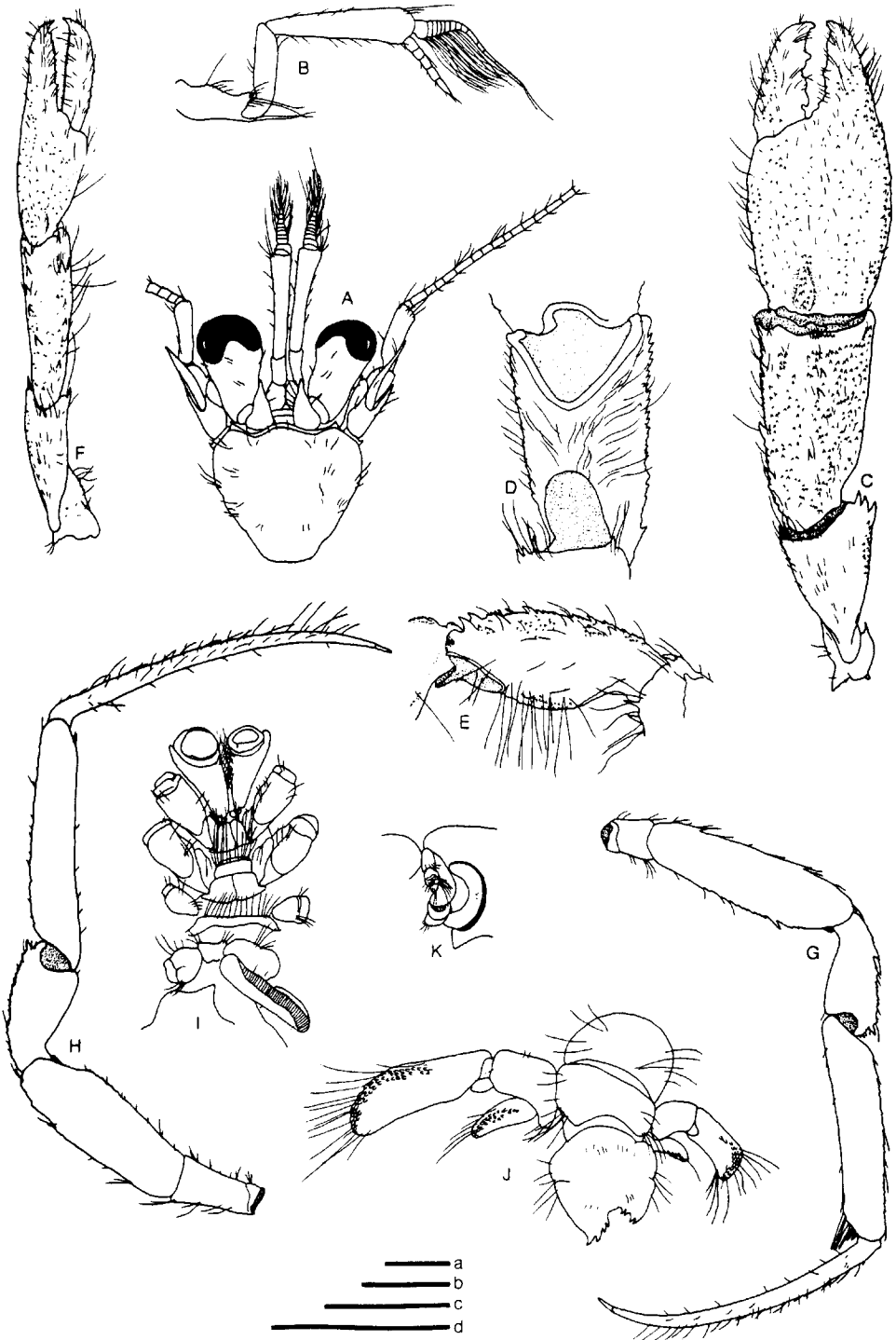
Colour.— Unknown.

Related organisms.— The specimens of *A. longispina* collected off Cabo de São Vicente (A. Milne Edwards & Bouvier, 1900) were found in the gastropod shells of *Turritella*, *Natica*, and *Nassa* (= *Hinia*). In the present collections, specimens of *A. longispina* were found inhabiting the gastropod shells of *Turritella biplicata* (2 specimens, MMSU- "AAK" station 1296), *Gibbula tumida* (1 specimen, MMSU- "AAK" station 1305), and *Cytharomorula* (= *Evokesia?*) sp. (1 specimen, NHRM 6999); and a pectinariid polychaete tube (MMSU- "AAK" 1296).

There is no external evidence of symbionts in any of the specimens examined.

Distribution.— *Anapagurus longispina* has been reported: in the northeastern Atlantic, off the Azores (A. Milne Edwards & Bouvier, 1894; as *A. laevis*), off southwest Portugal (A. Milne Edwards & Bouvier, 1900; as *A. laevis* and *A. laevis* var. *longispina*.— Türkay, 1976; as *A. laevis*), and in Seine Seamount, east off Madeira Island (Bouvier, 1922).— in the Mediterranean Sea, off Azores (Forest, 1965), off Toulon (A. Milne Edwards & Bouvier, 1900; as *A. laevis*), and in the Aegean Sea (Kocatas, 1981). The following localities are new records of *A. longispina*: in the Mediterranean Sea, Golfo of Valencia, Strait of Sicily, and off the coasts of Malt, Sinai and Israel; and in the southeastern Atlantic, off Port Alexander, Angola. Depth range: Forest (1965) recorded the bathymetric range of *A. longispina* as 99–445 m; the present record of 57 m shows that this species also occurs in shallower waters.

Fig. 16. *Anapagurus longispina* A. Milne Edwards & Bouvier, 1900. ♂ (SL = 2.0 mm), "Talisman", 39°53'N, 10°52'W, MCZ 6580: A, shield and cephalic appendages; B, right antennule (lateral view); C, right cheliped (dorsal view); D, carpus of same (ventral view); E, carpus of same (ventromesial view); F, left cheliped (dorsal view); G, left 2nd pereopod (mesial view); H, left 3rd pereopod (mesial view); I, sternum; J, extremity of abdomen, uropods and telson; K, left sexual tube (lateral view). Scales equal 1.0 mm: a: K; b: A, C-I; c: B; d: J.



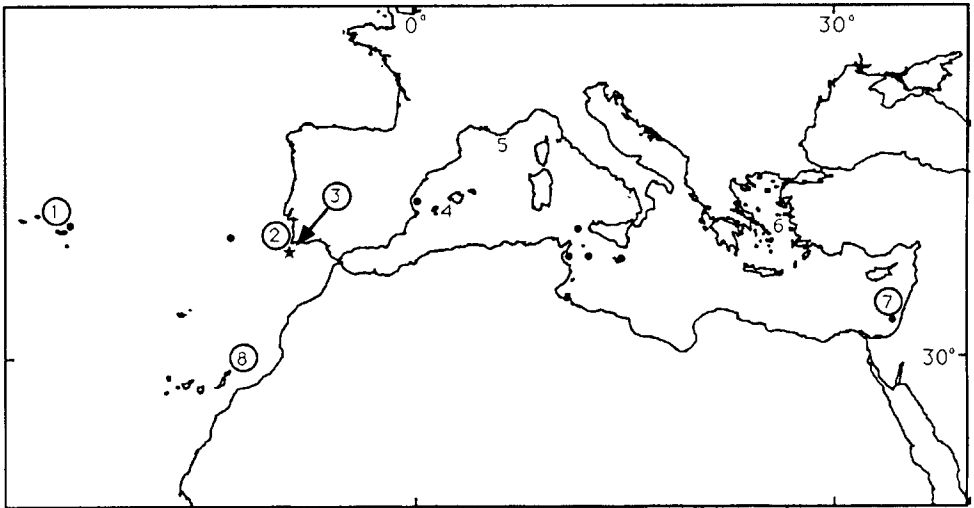


Fig. 17. Distribution of *Anapagurus longispina* A. Milne Edwards & Bouvier, 1900. Star: type locality. Solid circles: based on present records. Numbers: based on previous records (circled numbers: material examined): 1-A. Milne Edwards & Bouvier, 1894 (as *A. laevis*); 2-Türkay, 1976 (as *A. laevis*); 3, 5-A. Milne Edwards & Bouvier, 1900 (as *A. laevis*); 4-Forest, 1965; 6-Kocatas, 1981; 7-Holthuis & Gottlieb, 1958; 8-Bouvier, 1922.

**Affinities.**— As have other congeners, *A. longispina* has been confounded with *A. laevis*. The relationship between the two species is inferred from the similarity observed between the strongly dilated corneae. *A. longispina* can be readily separated from *A. laevis* by the depressed, dorsal carpal surface of the right cheliped of the former, the much longer and slender ultimate antennular segment, the sternal anterior lobes of the 2nd pereopods not extended distolaterally, and, in males, the much longer ventromesial distal spines of the propodi of the 2nd pereopods. Ocular acicles that terminate in long marginal spine easily distinguish *A. longispina* from other species of *Anapagurus*.

**Remarks.**— A. Milne Edwards & Bouvier (1900) observed the specimens of *A. laevis* collected by the "Travailleur" and the "Talisman" and noticed a male with long ocular acicles and named it *A. laevis* var. *longispina*. In one of the specimens collected by the "Travailleur" off Cap Sicié, near Toulon (station 9) Forest (1965) found several diagnostic characters that convinced him that *longispina* was a distinct species.

My examination of the collections of earlier authors has shown that certain specimens of *A. longispina* have been misidentified as *A. laevis*: A. Milne Edwards & Bouvier, 1892 and 1894 (one male collected at station 226 by the "Hirondelle", MOM 380157), 1900 (three males collected at station 2 by the "Talisman": (one) MCZ 6580 and (two) USNM 22922); Holthuis & Gottlieb, 1958 (three specimens collected in Haifa Bay and off Atlit, Israel, RMNH D 13728, 13736, and 13744); and Türkay, 1976 (one ovigerous female collected at station 9c90 by the "Meteor," SMF 4799).

Forest (1965) and Zariquiey Alvarez (1968) incorrectly cited figures 12 and 13 in the synonymy of A. Milne Edwards & Bouvier 1900's work; the latter authors did not illustrate the new subspecies of *A. laevis*.



*Anapagurus bonnieri* Nobili, 1905  
(figs. 18, 19)

*Anapagurus Bonnieri* Nobili, 1905: 239; 1906b: 89-91, pl V: figs. 19, 19a, not 19b (type locality: "J. Bonnier & Ch. Pérez Mission" station XLVII: from 25°10'N, 55°10'E to 24°55'N, 54°40'E, Persian Gulf, 12.8-27.4 m, on pearl oyster bank).

*Anapagurus bonnieri*; Gordan, 1956: 302 (listed); Lewinsohn, 1969: 87, fig. 15; Vine, 1986: 108.

*Anapagurus* sp.; Haig & Ball, 1988: 179, fig. 9.

Material.— Types not examined. **Red Sea:** 4 ♂♂ [1.3-2.0], 1 ovig. [1.7], off Dahlak Archipelago, Ethiopia, 15°35'30"N, 40°40'30", 12.8-14.6 m, 23.x.1965, TAU 1931. **Indonesia:** 1 ♂ [1.4], 2 ovig. [1.2, 1.4], "Alpha Helix" Saparua station 1, off Pulau Saparua, 3°36'S, 128°39.5'E, 5-7 m, on white sand, 29.v.1975, collector E.E. Ball, NIOJ.

Diagnosis.— Shield approximately as long as broad. Rostrum slightly exceeding lateral projections. Lateral projections with short submarginal spine.

Ocular peduncles approximately  $\frac{3}{4}$  length of shield, with corneae slightly dilated. Ocular acicles narrowly triangular, with strong submarginal spine. Interocular plate unarmed.

Antennular peduncles overreaching ocular peduncles by approximately  $\frac{3}{4}$  length of ultimate segment. Ultimate segment exceeding length of penultimate segment by approximately  $\frac{1}{3}$  own length, with 1 dorsolateral, short seta distally, ventral margin with row of tufts of setae, each tuft composed of 1 short seta between 2 long setae.

Antennal peduncles slightly exceeding or equaling length of ocular peduncles. Antennal acicles usually reaching to proximal margin of corneae.

Right cheliped with moderately broad chela. Dactyl  $\frac{1}{3}$  to  $\frac{3}{4}$  length of palm, with granules, larger near dorsomesial margin and tufts of long setae; dorsal surface slightly elevated in midline. Palm equaling or slightly exceeding length of carpus with dorsomesial margin with well-developed, granular ridge (spinulose ridge in larger specimens) and tufts of moderately long setae; dorsal surface somewhat convex, with granules (more numerous and larger near mesial margin) and tufts of short setae and long, prominent, granular ridge near dorsomesial margin proximally; dorsolateral margin well delimited, with row of granules increasing in size on fixed finger but not extending to claw; dorsoproximal margin with weakly developed, mesial and lateral lobes; all surfaces with scattered tufts of short setae; ventroproximal margin with skewed, median, subrectangular sinus and 2 small, slightly calcified sinuses. Carpus slightly exceeding length of merus, inflated; dorsomesial margin with row of closely spaced, acute spines and tufts of moderately long, stiff setae; dorsomesial distal angle produced into moderately large subtriangular structure, with a more raised ventral side; dorsodistal margin without triangular projection adjacent to dorsomesial distal angle; dorsal surface glabrous; dorsolateral margin with 1 acute spine on distal half, dorsolateral distal angle produced into small, subcircular lobe; mesial face slightly compressed, with tufts of moderately long setae; ventromesial margin subconical in mesial view; ventral surface granular and with tufts of long setae, short ventral length between deep, subtriangular, ventrodistal margin and deep, subcircular, ventroproximal margin; lateral face convex, unarmed. Dorsal margin of merus

with row of tufts of moderately long setae and partially obscured, strong distal spine; ventromesial margin with acute distal spine (small specimens) or tubercle (large specimens), and well-developed, tuberculate protuberance; ventrolateral margin with 3 or 4 strong spines (small specimens) or tubercles (large specimens); ventral surface with numerous tubercles and tufts of long, stiff setae. Ischium with 1 spinule on ventrolateral margin partly covered by short setae; ventromesial margin unarmed but with tufts of long, stiff setae. Coxae of chelipeds with ventrolateral distal angle unarmed.

Dactyl of left cheliped smooth but with tufts of moderately long setae. Dorsomesial and dorsolateral margins of carpus, each with 3 or 4 strong, widely spaced spines.

Ambulatory legs with dactyls exceeding propodi by approximately  $\frac{1}{6}$  own length, with dorsomesial row of closely spaced, short, stiff setae; mesial faces each with row of closely spaced, stiff setae near ventral margin; lateral faces each with row of widely spaced setae near unarmed ventral margin. Propodi exceeding carpi  $\frac{1}{3}$  to  $\frac{1}{2}$  own length; dorsal surfaces each with row of short setae; mesial and lateral faces each with row of short setae near ventral margin; ventromesial distal angle with 1 short spine. Carpi approximately  $\frac{2}{3}$  length of meri; dorsal surfaces with row of 5-7 strong spines (2nd) or 2 or 3 strong spines (3rd, small specimens), occasionally with 4 or 5 short spines and 2 distal strong spines (3rd, large specimens), and row of tufts of short stiff setae. Ventral margin of meri with 1 or 2 spinules on distal half (2nd) or unarmed (3rd) and row of tufts of short setae. Lobes of sternite of 2nd pereopods unarmed, distally rounded. Anterior lobe of sternite of 3rd pereopods subrectangular to subcircular; anterior margin with tufts of long setae.

Males with well-developed, left sexual tube, recurved upward to level of coxa; coxa of right 5th pereopod with gonopore on distoventral surface partly covered by tufts of long setae; three uniramous pleopods. Distal protopodal lobe of right uropod subequal to length of endopod.

Telson with asymmetrical posterior lobes separated by narrow deep cleft; terminal margins each with 2 to 4 strong spines; lateral margins unarmed but with tufts of long setae.

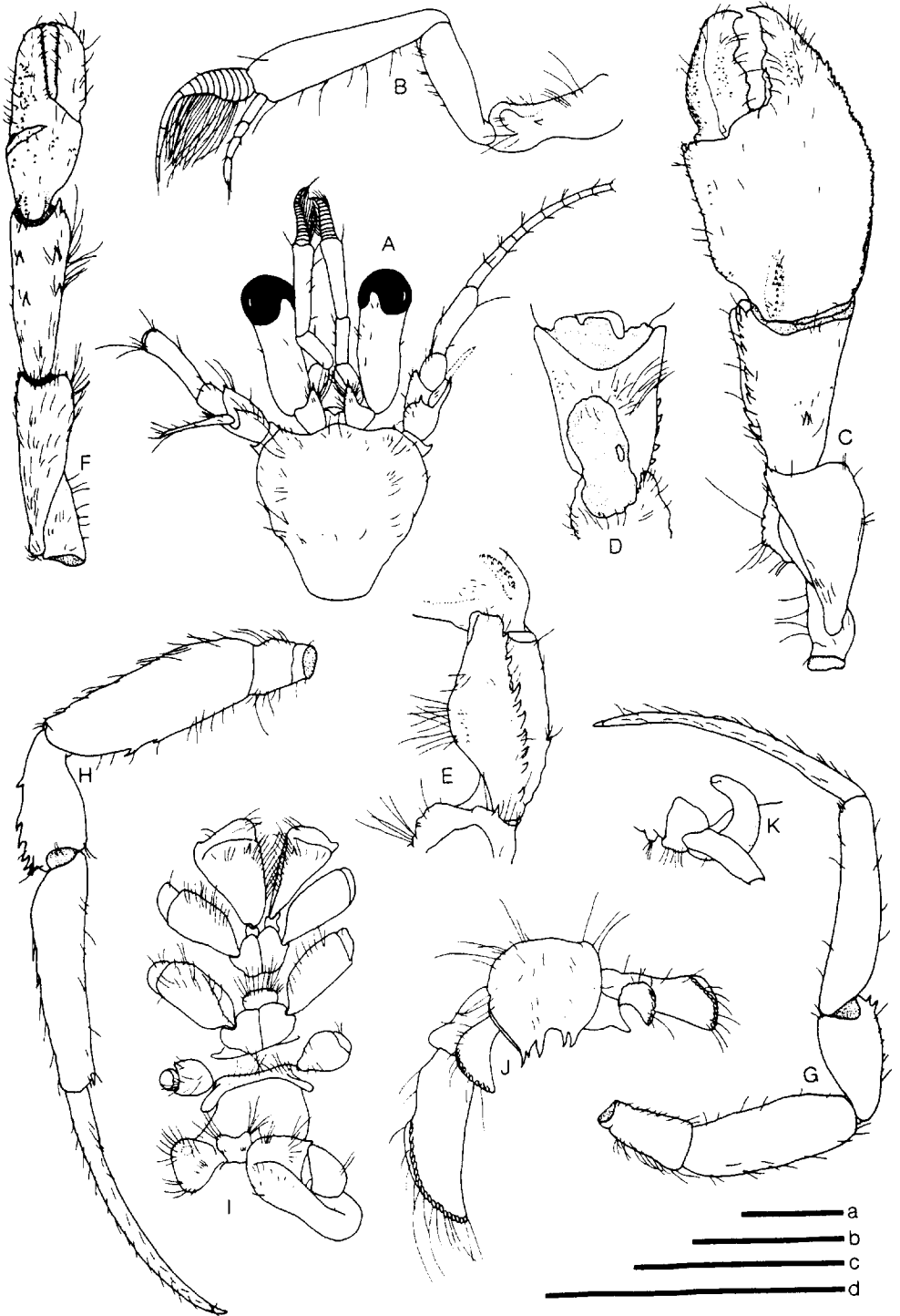
Colour.— "Basically transparent except for abundant white chromatophores" (Haig & Ball, 1988: 179; as *Anapagurus* sp.)

Behaviour.— "They [these hermit crabs] can take great leaps backwards (6-8 cm) and move very rapidly over the sand when frightened" (Haig & Ball, 1988: 179; as *Anapagurus* sp.).

Distribution.— In addition to the type locality, *A. bonnieri* has been collected off the Dahlak Archipelago (Ethiopia), Red Sea and off Pulau Saparua, Indonesia. Depth range: 5-15 m.

Affinities.— *Anapagurus bonnieri* shares a number of characters with *A. pusillus*,

Fig. 18. *Anapagurus bonnieri* Nobili, 1905. A-I: ♂ (SL = 2.0 mm), 15°35'30"N, 40°40'30"E, Red Sea, ISRSE 1931: A, shield and cephalic appendages; B, left antennule (lateral view); C, right cheliped (dorsal view); D, carpus of same (ventral view); E, carpus of same (mesial view); F, left cheliped (dorsal view); G, right 2nd pereopod (mesial view); H, right 3rd pereopod (mesial view); I, sternum. J, K: ♂ (SL = 1.4 mm), "ALPHA HELIX" Saparua station 1, 3°36'S, 148°39.5'E, NIOJ: J, uropods and telson; K, left sexual tube (lateral view). Scales equal 1.0 mm: a: K; b: A, C-I; c: B; d: J.



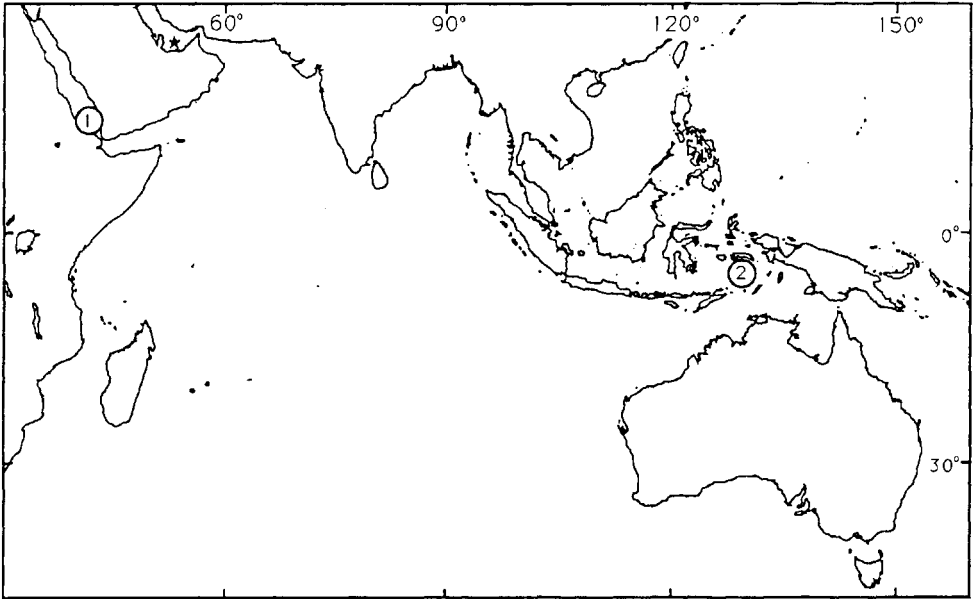


Fig. 19. Distribution of *Anapagurus bonnieri* Nobili, 1905. Star: type locality. Circled numbers: based on previous records, material examined: 1-Lewinsohn 1969; 2-Haig & Ball, 1988 (as *Anapagurus* sp.).

*A. breviaculeatus* and *A. alboranensis* spec. nov., however the former taxon is easily separated from the other three by its longer rostrum, which exceeds the lateral projections; the right cheliped with the dorsoproximal margin of the palm with weakly developed mesial and lateral lobes, the dorsodistal margin of the carpus lacking the projection adjacent to the dorsomesial distal angle, and the subconical ventromesial margin of the carpus in mesial view.

Remarks.— Lewinsohn (1969) mentioned that Nobili (1906b) erroneously illustrated a second pereopod (pl. V: fig. 19b) showing its dactyl with a long groove, a character that I too found absent in all of the specimens of *A. bonnieri* that I examined.

In their study of hermit crabs from northern Australian and eastern Indonesian waters, Haig & Ball (1988) listed a number of specimens from Pulau Saparua (Indonesia) as *Anapagurus* sp. I have been able to reexamine these and find that they are *A. bonnieri*.

*Anapagurus breviaculeatus* Fenizia, 1937  
(figs. 20, 21)

*Anapagurus laevis*; Bouvier, 1922: 31 (in part; see remarks); Holthuis & Gottlieb, 1958: 72 (in part; see remarks).

*Anapagurus breviaculeatus* Fenizia, 1937: 25-28, figs. 17-19 (type locality: off La Pietra, from off Island of Nisida to the Gulf of Pozzuoli, Italy; 5-15 m); Bouvier, 1940: 147, 148, fig. 101 (see remarks); Zariquiy Alvarez, 1955: 402; 1968: 257 (listed; see remarks); Gordan, 1956: 302 (listed); Balss, 1957: 1698 (listed); Forest, 1958: 100; 1965: 356-359, figs. 13, 16-18; 1967: 7; Pike & Williamson, 1958: 7, 8,

figs. 39-41; 1960: 525-528, fig. 8; Dechancé, 1962: 373, fig. 5; Peres & Picard, 1964: 63, 71; Hazlett, 1968b: 247, 248, fig. 5; Guille, 1971: 102, 111, 113, 119; Stevcic, 1972: 102, 103; Pastore, 1972: 107 (listed); Salmon, 1983: 148; García Raso, 1984: 259; 1985: 14 (listed); Ingle, 1985: 764 (listed); Ros, Romero, Ballesteros & Gili, 1985: 259.

*Anapagurus breviaculatus*; Forest, 1965: figure legends for figs. 13, 16-18; Kocatas, 1981: 162 (misspelling of *A. breviaculeatus*).

Material.— ♂ (carapace length=4.6 mm), off La Pietra, from off Island of Nisida to the Gulf of Rozzuoli, Italy, 5-15 m, 1936?, Museo Zoologico della R. Università di Napoli; not examined. **Northeastern Atlantic:** 1 ovig. [2.2], "Flor da Ponte" station 1.655, off NW Spain, Ría de Arosa, 0.2 km south off Los Mezos Light, 42°30.5'N, 08°55.8'W, 17 m, 24.vii.1964, collector L.B. Holthuis, USNM 121793. **Mediterranean Sea: Balearic Sea:** 1 ♂ [3.6], 3 ovig. [2.2-2.8], Bahía de San Antonio, Ibiza, 45.7 m, 1871, collector A. Lindahl, NHRM 6965; 7 ♂♂ [1.7-3.7], 3 ♀♀ [1.7-2.7], 2 ovig. [2.8, 2.9], Bahía de San Antonio, Ibiza, 45.7 m, 1871, collector F. Söderlund, NHRM 12061; 4 ♂♂ [1.5-3.6], 2 ♀♀ [2.0], 1 ovig. [2.8], off Formentera, 45.7 m, 1871, collector F. Söderlund, NHRM 12056; 2 ♂♂ [2.0, 2.8], 3 ♀♀ [1.5-2.2], off Formentera, 54.9 m, 1871, collector F. Söderlund, NHRM 12057; 1 ♂ [1.5], 1 ♀ [2.8], 1 ovig. [2.9], off Formentera, 64 m, 1871, collector F. Söderlund, NHRM 12058; 2 ♂♂ [2.9, 3.6], 3 ♀♀ [2.3-2.8], off Formentera, 73.2 m, 1871, collector F. Söderlund, NHRM 12059; 2 ♂♂ [2.6, 3.2], off Formentera, 91.4 m, 1871, collector F. Söderlund, NHRM 12060. **Bahía de Cadaqués:** 4 ♂♂ [0.7-1.2], 1 ♀ [0.8], 80-100 m, 7-15.viii.1949, collector L. B. Holthuis, RMNH D 6775; 1 ♀ [1.6], 20-50 m, 11-18.viii.1954, collector L.B. Holthuis, RMNH D 10285; 1 ovig. [1.0], 10-25 m, 31.vii.1957, collector L.B. Holthuis, RMNH D 12280; 3 ♂♂ [0.8-1.2], off Isla Arenella, ≈ 45 m, 1.viii.1957, collector L.B. Holthuis, RMNH D 12281; 1 ♂ [1.9], off Playa del Ros, 0-0.5 m, bottom of seagrass, 1.viii.1957, collector L.B. Holthuis, RMNH D 12282; 1 ♂ [1.7], off Playa d'En Pere, 0-1 m, bottom of seagrass, 31.vii.1957, collector L.B. Holthuis, RMNH D 12283; 1 ♂ [2.8], 1 ♀ [1.5], 1 ovig. [1.2], 20-30 m, 14.viii.1959, collector L.B. Holthuis, RMNH D 14877; 1 ♀ [1.9], Cala Jugadora, south of Cabo de Creus, bottom of seagrass, 17.viii.1959, collector L.B. Holthuis, RMNH D 14878; 1 ♂ [1.5], off Playa del Ros, 0-1 m, bottom of seagrass, 13.viii.1959, collector L.B. Holthuis, RMNH D 14879; 1 ♂ [1.0], off Farallons, 20-30 m, 12.viii.1959, collector L.B. Holthuis, RMNH D 14881; 1 ♂ [2.9], 1 ovig. [2.3], off Playa d'En Pere, 0-1 m, bottom of seagrass, 27.vii.1961, collector L.B. Holthuis, RMNH D 16587; 2 ♂♂ [2.2], 1 ♀ [1.8], 30 m, coarse sand, 2.viii.1961, collector L.B. Holthuis, RMNH D 16588; 3 ovig. [1.0-2.1], Port Lligat, ≈30 m, sandy bottom, 1.viii.1961, collector L.B. Holthuis, RMNH D 16589; 5 ♂♂ [1.5-2.9], 1 ♀ [1.3], 2 ovig. [2.1, 2.5], 30-40 m, coarse sand, 27.vii-2.viii.1961, collector L.B. Holthuis, RMNH D 16590. **Ligurian Sea:** 1 ♂ [3.2], "Hirondelle" station 1262, off Monaco, 43°43'N, 7°25'20"E, 48 m, 15.v.1902, MOM 380834; 2 ♂♂ [2.6, 2.7], off Sori, Italy, 45.7 m, x.1887, collector H. Théel, NHRM 6951; 2 ♂♂ [2.3, 2.7], off Sori, Italy, 36.6-54.9 m, 3.x.1887, collector H. Théel, NHRM 13178; 1 ovig. [1.9], off Cape Caccia, NW Sardinia, 8 m, bottom of gross sand, 9.v.1982, collector B. Dittrich, RMNH D 350; 1 ♂ [1.0], 1 juvenile [0.6], off Cape Caccia, NW Sardinia, 11.5 m, sandy bottom, 19.viii.1982, collector B. Dittrich, RMNH D 371; 1 juvenile [0.6], off Cape Caccia, NW Sardinia, 25 m, sand bottom, 6.ix.1982, RMNH D 4216. **Tyrrhenian Sea:** 2 ♂♂ [1.9, 2.0], 1 ovig. [2.2], off Naples, MOM 382513; 2 ♂♂ [1.6, 2.5], 2 ovig. [1.3, 1.9], off Villa Rocca Romana, Naples, 15 m, 8.v.1959, collected by Stazione Zoologica di Napoli, RMNH D 14880; 1 ♂ [2.3], Bocca Piccola, Capri, 80-100 m, 17.v.1959, collected by Stazione Zoologica di Napoli, RMNH D 14882; 1 ♂ [2.1], off east coast of Sardinia, Italy, 39°08'N, 08°20.2'E, 10 m, 5.iv.1972, collector G. Orel, CF 387. **Gulf of Taranto:** 1 ♂ [1.9], 1 ovig. [2.0], Porto Cesareo, 40°15'N, 17°54'E, collector Larenzan, MNHN 3166; 1 ♂ [2.3], 1 ovig. [1.9], off Island of Eolie, 11.vi.1974, collectors C. Frogia, G. Gianetti & B. Antolini, IRPEM D392. **Strait of Sicily:** 9 ♂♂ [2.5-3.4], 1 ♀ [2.0], 1 ovig. [2.3], "AAK" station 1261, 37°26.8'N, 12°11.6'E, 57 m, sandy clay bottom, 24.iv.1978, collector V.V. Murina, MMSU; 3 ♂♂ [2.3-3.3], 1 ♀ [2.0], "AAK" station 1262 (55), 37°40.0'N, 12°03.0'E, 21 m, clayed sand bottom, 24.iv.1978, collector V. V. Murina, MMSU; 1 ovig. [2.7], "AAK" station 1296, 37°30.7'N, 12°06.5'E, 86 m, sandy bottom, 10.ix.1979, collectors V.V. Murina & V.D. Tchukhtchin, MMSU; 1 ♂ [3.5], 2 ♀♀ [2.7], 1 ovig. [2.6], "AAK" station 1297, 37°28.0'N, 12°12.0'E, 62 m, sandy bottom, 11.ix.1979, collectors V.V. Murina & V.D. Tchukhtchin, MMSU; 2 ♂♂ [2.9, 3.2], 1 ovig. [2.2], "AAK" station 1298, 37°26.3'N, 12°10.5'E, 55 m, sandy bottom, 11.ix.1979, collectors V.V. Murina & V.D. Tchukhtchin, MMSU; 1 ovig. [1.8], "AAK" station 1299, 37°28.9'N, 12°12.0'E, 62 m, sandy bottom, 11.ix.1979, collec-

tors V.V. Murina & Sviridova, MMSU; 2 ♂♂ [2.2, 2.9], 1 ♀ [2.9], "AAK" station 1398, 37°23.6'N, 12°16.5'E, 70 m, sandy bottom, 7.ix.1979, collectors V.V. Murina & V.D. Tchukhtchin, MMSU. **Off East of Tunisia:** 2 ♂♂ [2.0, 2.4], "AAK" station 1208 (159), 35°23.2'N, 11°56.4'E, 62 m, sandy bottom, 9.vi.1974, collector V.V. Murina, MMSU; 2 ♂♂ [2.0, 2.6], "AAK" station 1265, 35°27.0'N, 11°39.3'E, 70 m, clayed sand bottom, 26.iv.1978, collector V.V. Murina, MMSU; 2 ♂♂ [1.7, 2.3], 1 ♀ [2.4], 1 ovig. [1.9], "AAK" station 1267, 35°10.0'N, 12°14.4'E, 50 m, sandy bottom covered with algae, 27.iv.1978, collector V.V. Murina, MMSU; 4 ♂♂ [2.1-2.6], 3 ♀♀ [1.6-2.1], "AAK" station 1268, 35°10.8'N, 12°34.0'E, 47-50 m, sandy bottom, 27.iv.1978, collector V.V. Murina, MMSU; 4 ♂♂ [1.9-2.4], 1 ♀ [2.1], 1 ovig. [2.4], "AAK" station 1269 (70), 35°13.0'N, 12°38.5'E, 57 m, sandy bottom, 28.iv.1978, collector V.V. Murina, MMSU; 1 ovig. [2.0], "AAK" station 1271, 35°46.2'N, 12°48.5'E, 70 m, bottom of organogenic sand, 29.iv.1978, collector V.V. Murina, MMSU; 4 ♂♂ [1.9-2.4], 4 ovig. [2.0-2.3], "AAK" station 1313, 35°17.2'N, 12°04.5'E, 53 m, sandy bottom covered with *Udotea*, 17.ix.1979, collector V.V. Murina, MMSU; 1 ♂ [2.6], "AAK" station 1314, 35°31.4'N, 12°02.6'E, 76 m, sandy bottom, 18.ix.1979, collector V.V. Murina, MMSU; 1 ♂ [2.2], 1 ovig. [2.6], 72 m, sandy bottom with fragments of *Lithothamnium*, 3.ix.1980, collectors V.V. Murina & V.D. Tchukhtchin, MMSU; 2 ♂♂ [1.9, 2.1], "AAK" station 1268, 35°10.8'N, 12°34.0'E, 47-50 m, sandy bottom, 27.iv.1978, collector V.V. Murina, MMSU. **Off east of Malta:** 2 ♂♂ [2.2, 2.9], 1 ovig. [1.6], "AAK" station 1273 (82), 35°56.3'N, 15°00.0'E, 91 m, sandy bottom with fragments of shells and *Lithothamnium*, 30.iv.1978, collector V.V. Murina, MMSU. **Adriatic Sea:** 3 ♂♂ [2.6-3.1], 2 ovig. [2.7, 3.0], Gulf of Manfredonia, Italy, 41°29.8'N, 15°59'E, 11 m, 7.vii.1974, collectors C. Froggia & G. Bombace, IRPEM D376; 2 ovig. [2.3, 2.6], 41°30.2'N, 15°58.7'E, 9 m, 7.vii.1974, collectors C. Froggia & P. Zucchini, IRPEM D377; 1 ♂ [2.5], 1 ovig. [1.9], 41°26.6'N, 16°05.4'E, 12 m, 5.vii.1974, collectors C. Froggia & G. Bombace, IRPEM D381; 2 ♂♂ [1.8, 2.5], 1 ovig. [1.2], off Rovinj, Yugoslavia, 5.vi.1962, RMNH D 19366; 3 ♂♂ [1.0-1.8], 1 ovig. [1.2], "F.B. Burin", off Rovinj, Yugoslavia, 28 m, 5.ix.1985, SMF 13908; 1 ♀ [1.3], "F.B. Burin", off Rovinj, Yugoslavia, 32 m, 10.ix.1985, collector Exk. Uni Frankfurt, SMF 13972; 1 ovig. [1.9], "F.B. Burin", off Rovinj, Yugoslavia, 36 m, 15.ix.1987, SMF 21923; 1 ♂ [2.3], "F.B. Burin", off Rovinj, Yugoslavia, 28 m, 17.x.1987, SMF 21924; 1 ♂ [1.8], "Sixten Bock", off Split, Yugoslavia, 30-35 m, bottom of sand and shells, iii.1932, NHRM 13571; 1 ♂ [1.6], "Sixten Bock", off Split, Yugoslavia, 30-35 m, bottom of sand and shells, 6.iv.1932, NHRM 13572. **Aegean Sea:** 1 ovig. [2.2], 39°04'N, 24°07'E, 20-25 m, 9.viii.1978, collector M. Türkay, SMF 12608; 1 ♂ [2.4], 39°19'N, 24°3'E, 6-8 m, 6.vii.1978, collector M. Türkay, SMF 12609; 1 ovig. [2.0], 39°21.6'N, 24°09.6'E, 20 m, 6.viii.1978, collector M. Türkay, SMF 12610; 1 ♂ [1.7], off Izmir, Turkey, 27.vi.1969, collector A. Kocatas, RMNH D 20709. **Off Israel:** 1 ♂ [3.0], sample 218, station 14, Haifa Bay, 18 m, 17.v.1955, collector E. Gottlieb, RMNH D 13724; 2 ♂♂ [1.0, 1.2], 2 ♀♀ [0.9, 1.0], sample 250, station 7→6 (7), Haifa Bay, 43, 2.viii.1955, collector E. Gottlieb, RMNH D 13725; 1 ♂ [1.0], sample 137, station 9, Haifa Bay, 42-44 m, 8.vii.1954, collector E. Gottlieb, RMNH D 13726; 1 ♂ [1.9], sample 213, station 4→3 (4), Haifa Bay, 38 m, 17.v.1955, collector E. Gottlieb, RMNH D 13727; 2 ♂♂ [0.8, 0.9], 1 ♀ [1.3], 1 ovig. [1.2], sample 374, station 5→6 (5), Haifa Bay, 55-60 m, 24.iv.1956, collector E. Gottlieb, RMNH D 13729; 1 ♂ [0.9], sample 171, station 14, Haifa Bay, 18 m, 30.xi.1954, collector E. Gottlieb, RMNH D 13730; 1 ♂ [1.0], sample 286, station 6→10 (6), Haifa Bay, 73 m, 21.ix.1955, collector E. Gottlieb, RMNH D 13731; 1 ♂ [0.9], 1 ♀ [0.8], 1 ovig. [1.1], sample 233, station 4→5 (5), Haifa Bay, 49 m, 7.vi.1955, collector E. Gottlieb, RMNH D 13732; 1 ♂ [1.4], sample 219, station 14, Haifa Bay, 18 m, 17.v.1955, collector E. Gottlieb, RMNH D 13733; 1 ovig. [1.3], sample 102, station 3, Haifa Bay, 31 m, 2.vi.1954, collector E. Gottlieb, RMNH D 13734; 1 ♂ [1.2], sample 112, station 7, Haifa Bay, 37-38 m, 3.vi.1954, collector E. Gottlieb, RMNH D 13735; 1 ♂ [1.1], sample 191 station 6→5 (6), Haifa Bay, 79 m, 5.iv.1955, collector E. Gottlieb, RMNH D 13736; 1 ♂ [1.2], 1 ovig. [1.2], sample 260, station 5→4 (4), Haifa Bay, 35 m, 18.viii.1955, collector E. Gottlieb, RMNH D 13737; 1 ♂ [1.8], 1 ovig. [1.5], sample 405, station 12→9 (12), Haifa Bay, 37-68 m, 13.v.1956, collector E. Gottlieb, RMNH D 13738; 1 ♂ [1.5], sample 257, station 9→8 (9), Haifa Bay, 42 m, 2.viii.1955, collector E. Gottlieb, RMNH D 13739; 1 ♂ [1.6], sample 123, station 10→6 (10), Haifa Bay, 73 m, 6.ix.1954, collector E. Gottlieb, RMNH D 13740; 1 ♂ [1.0], sample 52, station 2, Haifa Bay, 18 m, 23.viii.1953, collector E. Gottlieb, RMNH D 13741; 1 ♂ [1.0], sample 694, off Atlit, 54 m, 9.ix.1948, collector A. Wirszubski, RMNH D 13743; 1 ♂ [1.2], sample 682, off Caesarea, 72 m, 2.viii.1948, collector A. Wirszubski, RMNH D 13745; 2 ♂♂ [1.2], sample 691, off Tel Aviv, 36 m, 4.viii.1948, collector A. Wirszubski, RMNH D 13746.

Diagnosis.— Shield slightly longer than broad. Rostrum slightly exceeded by lateral projections. Lateral projections with short submarginal spine.

Ocular peduncles approximately  $\frac{3}{4}$  length of shield; with corneae slightly dilated. Ocular acicles subtriangular, terminating in short submarginal spine. Interocular plate unarmed.

Antennular peduncles exceeding distal margin of corneae, approximately by  $\frac{3}{5}$  length of ultimate segment. Ultimate segment exceeding length of penultimate segment by approximately  $\frac{1}{3}$  own length, with dorsolateral row of very short setae and 1 distal, moderately long seta; ventral margin with row of very short setae; basal segment with lateromedial and laterodistal (occasionally bifid) spines.

Antennal peduncles slightly exceeding distal margin of corneae. Antennal acicles reaching corneae proximally, with small terminal spine.

Right cheliped with moderately narrow chela. Dactyl approximately  $\frac{3}{4}$  length of palm, ventrally curved, strongly so in adult males; subcircular in cross section, with no ridges. Palm subequal to length of carpus, dorsomesial margin with granular ridge on proximal half; dorsal surface slightly convex, with scattered granules and short setae and with spinose ridge near dorsomesial margin proximally, prominent in females but almost obsolete in males; dorsolateral margin with granules (males) or spinules (females) becoming obsolete near claw; dorsoproximal margin with weakly developed mesial and lateral lobes; ventroproximal margin with skewed, median, subquadrate sinus. Carpus exceeding length of merus by approximately  $\frac{1}{4}$  own length; dorsomesial margin with irregular row of numerous short spines (males) or fewer but stronger spines (females); dorsomesial distal angle produced into concave, subrectangular lobe; dorsodistal margin with a projection adjacent to dorsomesial distal angle, triangular (females and immature males) or roundish (adult males) dorsolateral margin with row of 4-10 widely spaced spinules (females and immature males) or unarmed (adult males); ventral surface inflated, with tufts of stiff setae, long in males or short in females; short ventral length between moderately deep, subcircular ventrodistal and ventroproximal margins; ventromesial margin subcircular in mesial view. Ventromesial margin of merus with prominent, spinose protuberance (males) or tubercles (females), and with 1 short distal spine; ventrolateral margin with 3 to 5 strong spines; dorsal margin with short distal spine (small specimens) or unarmed (large specimens). Ischium with 1 spinule on ventrolateral margin partly covered by tufts of long, stiff setae. Coxae of chelipeds with ventrolateral distal angle unarmed.

Dactyl of left cheliped smooth but with tufts of moderately long setae. Dorsomesial margin of carpus with row of 5 to 7 strong, widely spaced spines; dorsolateral margin with row of 3 or 4 strong, widely spaced spines.

Dactyls of ambulatory legs exceeding length of propodi by approximately  $\frac{1}{4}$  own length, with dorsomesial row of closely spaced, moderately long setae and ventromesial row of closely spaced, short, stiff setae. Propodi exceeding length of carpi by approximately  $\frac{1}{2}$  own length; ventromesial distal angle with corneous spines, 2-4 moderately long (2nd pereopods, males), 1 or 2 short (2nd pereopods, females), or unarmed but with stiff setae (3rd pereopods, both sexes). Carpi  $\frac{2}{3}$  length of meri; dorsal margins with 4-9 spinules (2nd) or serrate and 1 distal spine (3rd). Meri unarmed or occasionally with 1 spinule on distal third, dorsally and/or ventrally (2nd). Lobes of sternite of 2nd pereopods unarmed, distally rounded. Anterior lobe