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# Discovery of a new micro-pagurid fauna (Crustacea: Decapoda: Paguridae) in the Lesser Antilles, Caribbean Sea

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## ABSTRACT

Six new monotypic genera and eight new species of hermit crabs of the family Paguridae Latreille, 1802 are fully described based on specimens obtained during two separate, intensive biodiversity studies on the islands of Guadeloupe, Curaçao, and Dominica in the Lesser Antilles, Caribbean Sea. The study in Guadeloupe utilized a broad variety of sampling techniques, including dredging, baited traps, and a SCUBA-operated vacuum device; in Curaçao and Dominica, a manned submersible was used. The high number of new taxa discovered is surprising given they were obtained in a relatively small area of the Antilles in habitats ranging in depth from shallow water (*c.* 1 m) to deep reefs (250 m). Tissue samples were extracted from most specimens for CO1 barcoding and other genetic analyses for future phylogenetic investigations. Gene sequences are reported to complement the morphological descriptions. The new species are unusual in their minute sizes, ranging 0.4-1.5 mm in shield length; and aspects of their morphology, in particular gill number and characteristics of male sexual tubes, which could not be clearly matched to any of the existing genera of Paguridae. The term “micro-pagurid” is introduced for this diverse, diminutive fauna of Paguridae (adult shield length  $\leq 1.5$  mm), discovered living in cryptic habitats and complex deep reef structures of these three islands. A brief, preliminary discussion of the possible significance of this micro-pagurid diversity, specialized morphology, and biogeography is included.

## KEY WORDS

Micro-Paguridae,  
hermit crabs,  
Guadeloupe,  
Curaçao,  
Dominica,  
new genera,  
new species.

## RÉSUMÉ

*Découverte d'une nouvelle faune de micro-pagures (Crustacea: Decapoda: Paguridae) des Petites Antilles en mer des Caraïbes.*

Six nouveaux genres monospécifiques et huit nouvelles espèces de bernard-l'ermite de la famille des Paguridae Latreille, 1802 sont décrits à partir des spécimens obtenus lors de deux campagnes distinctes d'échantillonnage intensif de la biodiversité à la Guadeloupe, à Curaçao et à la Dominique, Petites Antilles, Mer des Caraïbes. En Guadeloupe, l'étude a utilisé une large gamme de techniques d'échantillonnage, incluant des dragages, des casiers appâtés et des aspirateurs à sédiments; à Curaçao et à la Dominique un sous-marin habité a été utilisé. Le grand nombre de nouveaux taxons découverts est surprenant, étant donné qu'ils ont été obtenus dans une région relativement limitée des Antilles dans des habitats répartis en eau peu profonde (*c.* 1 m) jusqu'aux récifs profonds (250 m). Des échantillons de tissus ont été extraits de la plupart des spécimens pour le séquençage du gène CO1 et d'autres analyses moléculaires pour de futures études phylogénétiques. Les nouvelles espèces sont inhabituelles par leur taille minuscule, la longueur de l'écusson céphalothoracique allant de 0,4 à 1,5 mm; de plusieurs caractéristiques morphologiques, en particulier le nombre de branchies et l'aspect des tubes sexuels mâles qui ne correspondent véritablement à aucun autre genre de Paguridae connu. Le terme de « micro-pagure » est introduit pour cette faune diverse et minuscule (écusson céphalothoracique adulte  $\leq 1,5$  mm) de Paguridae découverte dans des habitats cryptiques et des structures complexes des récifs profonds de ces trois îles. Une discussion brève est proposée quant à la nature de la diversité de ces micro-pagures, de leur morphologie spécialisée et de leur biogéographie.

## MOTS CLÉS

Micro-pagure,  
bernard-l'ermite,  
Guadeloupe,  
Curaçao,  
Dominique,  
genres nouveaux,  
espèces nouvelles.

## INTRODUCTION

Hermit crabs or Paguroidea Latreille, 1802 (sensu McLaughlin *et al.* 2007), are common inhabitants of marine and semi-terrestrial habitats where they are easily recognized by their relatively large body size and the conspicuous shelters they adopt for protection. Among the majority of paguroids, adult body size, as measured by cephalic shield length (sl), well exceeds 1 mm, and at least one species, *Tisea grandis* Morgan & Forest, 1991, can grow to an extraordinarily large shield length of 58.8 mm. Thus, paguroids are considered part of the macrobenthos, i.e. benthic organisms exceeding 1 mm in length (Lincoln *et al.* 1982). In the last two decades, however, a number of genera and species have been described, often with names suggestive of their small size, sometimes for tiny species with shield lengths that do not exceed 1.5 mm, in one not exceeding 1 mm. Examples of these minute animals, all distributed in the North to Indo-West Pacific regions, and their size ranges, are: *Pygmaeopagurus hadrochirus* McLaughlin, 1986 (sl 0.6-0.9 mm); *Nanopagurus reesei* McLaughlin, 1986 (transferred to *Anapagrides* de Saint Laurent-Dehancé, 1966; see McLaughlin & Sandberg [1995]) (sl 0.7-1.7 mm); *Micropagurus devaneyi* McLaughlin, 1986 (sl 1.1-1.4 mm), and *M. bijdeleyi* Lemaitre, 2010 (sl 1.4-1.6 mm); *Scopaeopagurus megalochirus* McLaughlin & Hogarth, 1998 (sl 0.34-1.07 mm); *Hachijopagurus rubrimaculatus* Osawa & Okuno, 2003 (sl 1.3-1.6 mm); *Pteropagurus spina* McLaughlin & Rahayu, 2006 (sl 1.2-1.3 mm), and *P. inermis* McLaughlin & Rahayu, 2006 (sl 1.2-1.6 mm), and *P. spinulocarpus* McLaughlin & Rahayu, 2007 (see also McLaughlin & Rahayu 2008a); *Pumilopagurus tuberculomanus* McLaughlin & Rahayu, 2008 (sl 1.1-1.4 mm), *Cestopagurus caeruleus* Komai & Poupin, 2012 (sl 1.2-1.9 mm),

*Trichopagurus asper* Komai & Poupin, 2012 (sl 1.4 mm), *Pagurixus annulus* Komai & Poupin, 2013 (sl 0.9-1.3 mm), and *P. europa* Komai & Poupin, 2013 (sl 0.9-1.5 mm). McLaughlin (1986) was the first to discuss the unusual minute size of species in her trilogy of Hawaiian monotypic genera, *Pygmaeopagurus* McLaughlin, 1986, *Nanopagurus* McLaughlin, 1986, and *Micropagurus* McLaughlin, 1986, and noted that they represent a group of highly specialized pagurids, the first shallow-water genera with male sexual tubes to be reported from the Hawaiian Islands. She documented that females of *Pygmaeopagurus hadrochirus* could be ovigerous at a remarkably small shield length of 0.6 mm, while bearing relatively few, large eggs, suggesting abbreviated larval development.

Among the western Atlantic Paguridae, several genera (e.g., *Enneobranchus* García-Gómez, 1988, *Iridopagurus* de Saint Laurent-Dehancé, 1966, *Nematopaguroides* Forest & de Saint Laurent, 1968, *Pagurus* Fabricius, 1775) are known to include species with adults that occasionally can have a shield length smaller than 1 mm. Perhaps the tiniest species in this region can be found among several of the 12 species of the *provenzano* group of *Pagurus*, which are known to occur abundantly in shallow-water habitats from the northeastern coast of the United States, Gulf of Mexico, and Caribbean to Argentina. These range in sl from 0.4 to 3.9 mm, although at least two of the species, *Pagurus carolinensis* McLaughlin, 1975 and *P. protuberocarpus* McLaughlin, 1982, have not been reported to grow above sl 1.4 mm (Lemaitre *et al.* 1982). Given the known abundance of “small to micro” mollusks (Bouchet pers. comm.) in the Caribbean islands of the Antilles, it would be expected that this large source of empty micro-shells is available for pagurids to exploit as housing, which in turn might lead to the existence of a greater pagurid diversity than known

to date. Regrettably, in order to test this expectation, targeted sampling for micro-habitats where these micro-mollusk or micro-pagurids might live has not been undertaken on large focused scales, until recently.

The opportunity to investigate in more detail the poorly known cryptic diversity of the pagurid fauna of the vast Antilles, came with two separate but parallel, intense modern research programs that included collection of voucher specimens, photographs, and gathering of tissue samples for DNA analyses. The first began in 2011 as a collaborative effort between the Smithsonian Institution and Substation Curaçao, known as Deep Reef Observation Program (DROP), to investigate and document deep-reef biodiversity using the manned submersible CURASUB, as well as long-term monitoring structures, to a depth of 300 m. Although this program has primarily focused on deep-reefs off Curaçao, sampling and submersible activities have been extended to Dominica, also in the Lesser Antilles. The second program began in 2012 in Guadeloupe, with an expedition known as KARUBENTHOS 2012, under the direction of the Muséum national d'Histoire naturelle, Paris (MNHN), in collaboration with Université des Antilles et de la Guyane, Pointe-à-Pitre (UAG) and Université Pierre-et-Marie-Curie, Paris (UPMC). This program sampled numerous cryptic habitats on this island from shallow-water to 150 m in depth, as part of an inventory of mollusks, decapod crustaceans, echinoderms and algae primarily from the “Parc national de la Guadeloupe”.

The study of the numerous diminutive hermit crab specimens obtained during KARUBENTHOS 2012 and DROP has revealed the existence of an unforeseen pagurid diversity at the generic and species level. Six new monotypic genera, each represented by its own new species, along with a new species of *Nematopaguroides* and *Pagurus* respectively, have been discovered, all with adults no larger than sl 1.5 mm and as small as sl 0.4 mm. All but one of the new species discovered have males bearing sexual tubes, and in cases where ovigerous females were found, they had few, relatively large eggs. In pagurids, when sexual tubes are present in the male, the morphological characters represented in these structures (paired, unpaired, size, length, etc.) are considered of critical diagnostic significance at the generic level (McLaughlin 2003). Herein we fully describe and illustrate all the new genera and species, discuss the possible meaning of the discovery of this micro-pagurid diversity in the Caribbean, and compare the findings in Guadeloupe to those in Curaçao. A significant number of other interesting or rare but previously known species of pagurids, some comparably small in size to the new taxa herein described, were also collected, and those are to be reported by us in a separate study.

## MATERIAL AND METHODS

### COLLECTIONS

#### *Curaçao and Dominica*

Samples from deep reef habitats in Curaçao were obtained using the 5-person CURASUB submersible operated by Substation Curaçao (see: <http://www.substation-Curacao.com>).

CURASUB is provided with two flexible, hydraulic arms, one of which is equipped with a suction hose, to obtain live specimens or substrates that may contain small specimens not easily visible by the naked eye from inside the CURASUB. One particular and unexpectedly productive source of specimens consisted of discarded glass bottles found to contain numerous dead micro-gastropod shells that were frequently inhabited by minute hermit crabs. Another was submersible-retrieved Autonomous Reef Monitoring Structures (ARMS), constructed and processed as described below. Sampled bottles and debris were placed by mechanical arm into buckets or nets attached to a platform in front of the CURASUB. ARMS samplers were enclosed in specially designed container boxes for submarine retrieval. Suctioned specimens were captured in a down-stream bucket equipped with filter screens. At the surface, samples were kept alive, sorted, and photographed after being chilled or frozen. Subsequently, each individual specimen or morphotype was fixed in 95% ethanol for identification, tissue was removed for genetic analysis, and samples were given a number with the prefix CURI (= Curaçao Invertebrate). Unless otherwise stated, all CURASUB dives were from east of the downline at the Substation Curaçao dock, in Bapor Kibra, Willemstad, and were thus given the same coordinates 12°04'59.51"N, 68°53'56.61"W, with only depth range varying.

ARMS samplers consisted of a tier of nine 23 × 23 cm gray, Type I PVC plates stacked and attached to a 35 × 45 cm base plate. The entire structure was affixed to the sea floor for 1–3 years, during which time it became colonized with marine organisms (see [http://www.pifsc.noaa.gov/cred/survey\\_methods/arms/overview.php](http://www.pifsc.noaa.gov/cred/survey_methods/arms/overview.php)). Hermit crab specimens obtained from ARMS in Curaçao deep reefs, were processed according to methods described in Leray & Knowlton (2015). Each individual specimen or morphotype from ARMS was treated similarly to those from the CURASUB, except that tissue samples for genetic analyses (CO1) were given the prefix BCURA (= Barcode Curaçao ARMS). All ARMS listed in the material examined were placed off the Substation Curaçao dock, and are given the same coordinates as for CURASUB dives, with only recovery date and depth varying. Specimens are deposited in the National Museum of Natural History, Smithsonian Institution, Washington DC (USNM), with some duplicates in MNHN.

#### *Guadeloupe*

The expedition to Guadeloupe, known by the acronym KARUBENTHOS 2012, took place 2–30.V.2012, and was a joint effort between the MNHN, the Parc national de Guadeloupe, the UAG, and the UPMC. The goal was to inventory mollusks, decapod crustaceans, echinoderms and algae. A range of habitats were sampled (mangroves, seagrass beds, sandy beaches, rubble, coral and sponge bottoms, marine caves, mangrove, open sand beaches) from intertidal waters to 160 m. Specimens were collected at various stations (sta) using SCUBA-operated brush baskets (sta GB), dredging (sta GD), or by hand collecting while snorkeling in intertidal to shallow water (sta GM), or SCUBA diving (sta GR) from 5–50 m. Baited traps (sta GN) and a SCUBA-operated

vacuum device (sta GS) were also used. A total of 270 stations were sampled. The documented list of the stations, including an interactive map, can be accessed through the MNHN repository of surveys (see <http://expeditions.mnhn.fr/campaign/karubenthos2012>). In the lab, specimens were photographed, tissue was removed for genetic analyses and deposition at MNHN, and each specimens or morphotype was assigned a number with the code prefix **MNHN-IU-2013**, following the methodology discussed by Puillandre *et al.* (2012). Specimens are deposited in MNHN, with some duplicates at USNM.

#### VOUCHERS, TISSUE SAMPLES AND SEQUENCE DATA

Tissue samples of Curaçao specimens for DNA Barcoding or other genetic analysis were deposited in the USNM Biorepository and those of Guadeloupe specimens in MNHN. Mitochondrial CO1 barcode gene sequences were obtained by standard protocols applied in the Smithsonian Laboratories for Analytical Biology (see Evans & Paulay 2012). Unaligned sequences for at least one type specimen of each new species were accessioned to GenBank along with archival data for the respective voucher specimens listed in Table 1. They are there as diagnostic identifiers for these species, whether used in future study or not.

#### PHOTOGRAPHY

Given extremely small sizes of the subject animals, normal color photography protocols in the field sometimes yielded images of suboptimal resolution. We none-the-less have included some of these given the established importance of color patterns in paguroids in general, and in micro-pagurids in particular. Field protocol for processing specimens in Curaçao and Dominica included taking digital color photographs of fresh specimens of each recognized species or morphotype, using a Nikon D800E digital camera equipped with a 60 mm macrolens and appropriate extension tubes to increase magnification. All specimens were posed on a copy stand below the surface of water-filled dishes with backgrounds of black felt, where they were obliquely illuminated by 5000°K artificial lighting. Photographs were identified by ULLZ registration numbers that were in turn cross-referenced to CURI, BCURI, and USNM numbers.

#### SYSTEMATICS, ABBREVIATIONS

The new genera and new species are arranged alphabetically. Terminology for descriptions generally follows that of McLaughlin (1997), but McLaughlin (2003) for definition of male sexual tube lengths. The ambulatory legs are equivalent to pereopods 2 and 3. Cephalothoracic somites are numbered I–XIII (five cephalic and eight thoracic), and thoracomeres are numbered I–VIII (three maxillipeds and five pereopods). Shield length (sl) measured from the tip of the rostrum to the midpoint of the posterior margin of the shield, provides an indication of animal size. The station data in material examined section is listed by date of collections. Other abbreviations are: ovig, ovigerous, and sta, station. The new taxa described herein, with collection site, deposition of genetic tissue/data and voucher specimens, are summarized in Table 1.

#### Institutions

MNHN	Muséum national d'Histoire naturelle, Paris;
UAG	Université des Antilles et de la Guyane, Point-à-Pitre;
UPMC	Université Pierre-et-Marie-Curie, Paris;
ULLZ	University of Louisiana – Lafayette Zoological Collections, Lafayette;
USNM	National Museum of Natural History, Smithsonian Institution, Washington DC.

#### SYSTEMATICS

##### Family PAGURIDAE Latreille, 1802

##### Genus *Leptopagurus* n. gen.

TYPE SPECIES. — *Leptopagurus rhabdotus* n. gen., n. sp., by present designation. Gender: masculine.

ETYMOLOGY. — The generic name is derived from the genus name *Pagurus*, combined with the Greek prefix *leptos*, which denotes something thin, small, in reference to the thin or elongated shape of the chelipeds and small size of specimens in the single species of this new genus.

DIAGNOSIS. — Eleven pairs of biserial phyllobranch gills, no pleurobranchs on somites X, XI (above pereopods 2 and 3). Rostrum triangular. Second maxilliped with stout propodus-dactyl (propodus height larger than length); third maxilliped ischium with accessory tooth. Chelipeds slender, subequal in length. Sternite of somite XI (thoracomer 6, pereopod 3) with subsemicircular anterior lobe. Pereopod 4 with single row of scales on propodal rasp, dactyl lacking preungual process. Pereopod 5 semi-chelate. Male with coxae of pereopods 5 symmetrical, with paired, subequal, stout, membranous sexual tubes; with unpaired, left pleopods 3–5. Female unknown. Telson nearly symmetrical, with distinct lateral indentations; terminal margins of posterior lobes weakly oblique, armed with spines.

DISTRIBUTION. — Known only from the type species collected in Curaçao, Caribbean Sea. Depth: 224 m.

#### REMARKS

This genus differs from other pagurid genera in a number of characters, most visibly the presence of paired male sexual tubes; the stout propodus-dactyl of the second maxillipeds; and the slender, subequal chelipeds, with clusters of elongate, capsulate setae on the ventral faces of meri.

##### *Leptopagurus rhabdotus* n. sp. (Figs 1–4; Table 1)

TYPE MATERIAL. — **Holotype.** ♂ 1.1 mm, Curaçao, ARMS 14, 224 m, 15.IX.2015, BCURA 0668, USNM 1297635 (ULLZ 16890). **Paratypes.** Curaçao: 1 ♂ 1.5 mm, ARMS 22, 224 m, 15.IX.2015, BCURA 1499, USNM 1297449 (ULLZ 16921); 1 ♂ 1.0 mm, CURASUB 15–26, Playa Forti, Westpoint, 12°22'4.8"N, 69°09'18"W, 124.6–198.4 m, 29.IX.2015, CURI 15048, USNM 1297279. Dominica: 1 ♂ 0.9 mm, Prince Rupert Bay, Portsmouth, near Picard Beach Cottage, CURASUB 16–12, 15 33'25.2576, 61 28'15.3804, 50–178 m, 8.III.2016, inside glass bottle, DOMnt 16016, USNM 1291967.

ETYMOLOGY. — The specific name is from the Greek *rhabdotos*, meaning striped, in reference to the striped color pattern of the chelipeds and ambulatory legs of this new species.

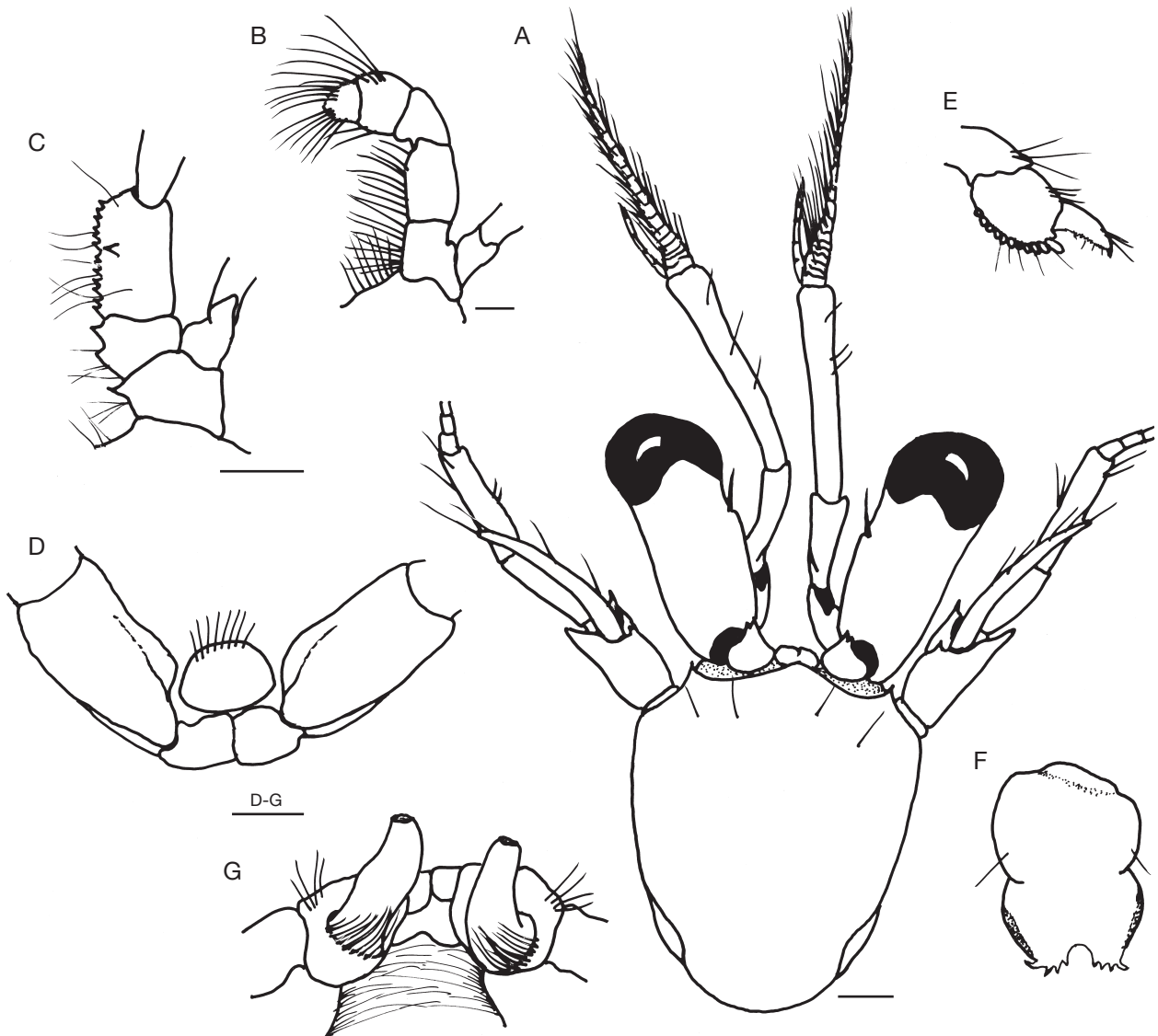


FIG. 1. — *Leptopagurus rhabdotus* n. gen., n. sp., holotype ♂ 1.1 mm, Curaçao, USNM 1297635: **A**, shield and cephalic appendages, dorsal view; **B**, left second maxilliped, external view; **C**, basis, ischium and merus of left third maxilliped, external view; **D**, sternite XI and coxae of third pereopods, ventral view; **E**, propodus and dactyl of right fourth pereopod, lateral view; **F**, telson, dorsal view; **G**, sternite XIII and coxae of fifth pereopods with sexual tubes, ventral view. Scale bars: A, 1 mm; B, 0.1 mm; C, 0.25 mm; D-G, 0.2 mm.

**DISTRIBUTION.** — So far known only from off Willemstad, Curaçao, and off Portsmouth, Dominica, in the Caribbean Sea. Depth: 50–224 m.

**HABITAT.** — Found in gastropod shells on ARMS and inside glass bottles.

#### DESCRIPTION

##### *Shield (Fig. 1A)*

Subovate, glabrous, at most with scattered setae anteriorly, about 1.2 times as long as broad; anterior margin between rostrum and lateral projections weakly concave; anterolateral margins sloping; posterior margin roundly truncate. Rostrum bluntly subtriangular, reaching slightly beyond level of lateral projections. Lateral projections subtriangular, each terminating in sharp spine.

##### *Ocular peduncles*

About 0.7 length of shield, glabrous except for dorsomesial distal bristle; corneas large but weakly dilated. Ocular acicles subtriangular, dorsal surface flat; terminating in bifid spine.

##### *Antennular peduncles*

Exceeding distal margins of cornea when fully extended by about 0.7 length of ultimate segment. Ultimate segment naked except for scattered short setae dorsally. Penultimate and basal segments naked; basal segment with blunt ventromesial angle, and small spine on lateral face.

##### *Antennal peduncles*

Exceeding distal margins of corneas when fully extended by about 0.8 length of fifth segment. Fifth and fourth segments

TABLE 1. — List of species, collection site, museum catalog number, ARMS or tissue number, and Barcode of Life Data Systems (BOLD) accession number of voucher specimens for which mitochondrial CO1 barcode gene sequences were obtained in this report (\*, holotype; \*\*, no tissue analyzed).

Genus/species	Collection site	Museum catalog no.	ARMS or tissue no.	BOLD no. (CO1)
Genus <i>Leptopagurus</i> n. gen.				
<i>Leptopagurus rhabdotus</i> n. gen., n. sp.	Curaçao	USNM 1297635*	BCURA 0668	RNHC002-16
	Curaçao	USNM 1297449, ULLZ 16921	BCURA 1499	RNHC003-16
	Curaçao	USNM 1297279	CURI 15048	—
	Dominica	USNM 1291967**	—	—
Genus <i>Nematopaguroides</i> Forest & de Saint Laurent, 1968				
<i>Nematopaguroides karukera</i> n. sp.	Guadeloupe	MNHN (several), USNM (several)**	—	—
Genus <i>Pagurellus</i> n. gen.				
<i>Pagurellus jenniferae</i> n. gen., n. sp.	Curaçao	USNM 1291918	BCURA 0670	RNHC005-16
	Curaçao	USNM 1297462	BCURA 0704	RNHC008-16
	Curaçao	USNM 1297636, ULLZ 16891	BCURA 0669	RNHC004-16
	Curaçao	USNM 1291920	BCURA 0671	RNHC006-16
	Curaçao	USNM 1291922	BCURA 0672	RNHC007-16
	Curaçao	MNHN-IU-2013-5564	BCURA 0966	RNHC011-16
	Curaçao	MNHN-IU-2013-5565	BCURA 0951	RNHC009-16
	Curaçao	MNHN-IU-2013-5566	BCURA 0964	RNHC010-16
	Curaçao	USNM 1297501	BCURA 0960	RNHC012-16
	Curaçao	USNM 1297446, ULLZ 16923	BCURA 1500	RNHC013-16
	Curaçao	USNM 1291921	BCURA 1501	RNHC014-16
Genus <i>Pagurina</i> n. gen.				
<i>Pagurina bifida</i> n. gen., n. sp.	Guadeloupe	MNHN-IU-2013-5643**	—	—
Genus <i>Paguriscus</i> n. gen.				
<i>Paguriscus robustus</i> n. gen., n. sp.	Guadeloupe	MNHN-IU-2013-4395**	—	—
Genus <i>Paguruncio</i> n. gen.				
<i>Paguruncio parvulus</i> n. gen., n. sp.	Curaçao	USNM 1297508*	BCURA 0952	RNHC015-16
	Curaçao	USNM 1297613	BCURA 1557	RNHC016-16
Genus <i>Pagurus</i> Fabricius, 1775				
<i>Pagurus abditus</i> n. sp.	Curaçao	USNM 1297485*	BCURA 0924	RNHC017-16
	Curaçao	USNM 1297441, ULLZ 16885	BCURA 0605	RNHC018-16
	Curaçao	USNM 1297489	BCURA 0780	RNHC019-16
	Curaçao	USNM 1292078	BCURA 2555	RNHC024-17
	Curaçao	USNM 1292079	BCURA 2754	RNHC025-17
Genus <i>Pusillopagurus</i> n. gen.				
<i>Pusillopagurus polulus</i> n. gen., n. sp.	Curaçao	USNM 1297496*	BCURA 0779	RNHC020-16
	Curaçao	USNM 1291925	BCURA 0632	RNHC021-16
	Curaçao	USNM 1291924	BCURA 1278	RNHC022-16
	Curaçao	USNM 1291923	BCURA 1556	RNHC023-16

unarmed except for scattered short setae or bristles. Third segment with small spine on ventrodistal angle. Second segment with dorsolateral distal angle produced into spine-like process slightly overreaching distal margin of third segment; dorsomesial distal angle with small spine. First segment unarmed. Antennal acicle not exceeding distal margin of cornea, broadly curving outward and terminating in strong spine, mesial margin with few setae or bristles. Flagella long, exceeding tips of chelipeds, with few short setae < 1 flagellar article in length.

#### Mouthparts (Fig. 1B, C)

Mandible with incisor process calcareous. Maxillule with internal and external lobes weakly produced, subequal, internal lobe with long terminal seta. Maxilla with endopod slender, slightly shorter than distal lobe of basal endite but overreaching distal margin of scaphognathite. First maxilliped with endopod distally spatulate. Second maxilliped (Fig. 1B) with relatively

stout propodus-dactyl, propodus height larger than length, dactyl nearly as long as propodus and equilaterally triangular. Third maxilliped (Fig. 1C) ischium with crista dentata consisting of row of short, sharp teeth, and one accessory tooth.

#### Right cheliped (Fig. 2A-C)

Chelipeds slender, subequal in length. Right cheliped glabrous except for scattered setae or bristles. Chela with dorsal and ventral surfaces smooth, lacking armature except for few minute low tubercles proximally on dorsal surface of fixed finger. Fingers each terminating in sharp corneous claw slightly overlapping when closed. Dactyl 0.7 length of palm, cutting edge with two large, unequal calcareous teeth, row of fused small teeth forming uneven edge distally; ventromesial face smooth. Fixed finger similar to dactyl except for cutting edge having two broader, lower calcareous teeth, dorsolateral margin weakly defined by microscopic tubercles continued to mid-portion of palm; ventromesial surface

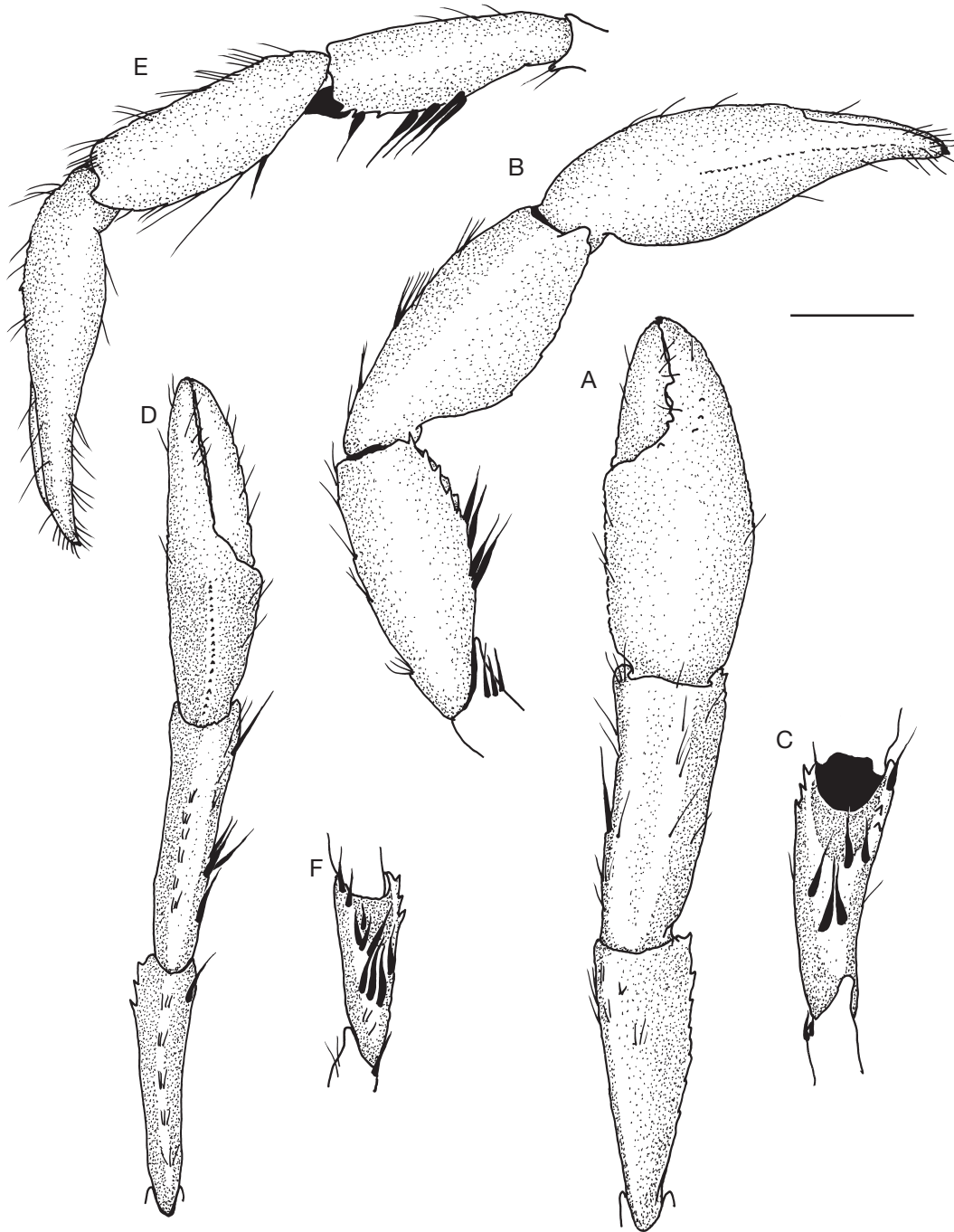


FIG. 2. — *Leptopagurus rhabdodus* n. gen., n. sp., holotype ♂ 1.1 mm, Curaçao, USNM 1297635: **A-C**, right cheliped, dorsal view (**A**), lateral view (**B**), merus ventral view (**C**); **D-F**, left cheliped, dorsal view (**D**), lateral view (**E**), merus, ventral view (**F**). Scale bar: 0.3 mm.

smooth. Palm 1.4 times as long as broad, about 0.7 as long as carpus, dorsal surface convex, unarmed except for scattered short setae, dorsolateral margin rounded proximally; dorsomesial margin rounded; ventral surface convex, glabrous. Carpus about 2.5 as long as broad, subequal to merus in length; dorsal surface weakly convex, with few moderately long setae or bristles; dorsomesial margin unarmed or with few small spines, dorsolateral margin lacking spines; lateral

face rounded, mesial face flat, nearly vertical; ventral surface smooth or with few weak low tubercles. Merus subtriangular in cross-section; ventral face with distinct capsulate setae clustered proximally, arranged in row on lateral and mesial margins (Fig. 2B, C), distolateral margin with row of sharp spines, distomesial margin with row of small mostly blunt spines. Ischium glabrous. Coxa with row of setae on ventromesial distal angle.

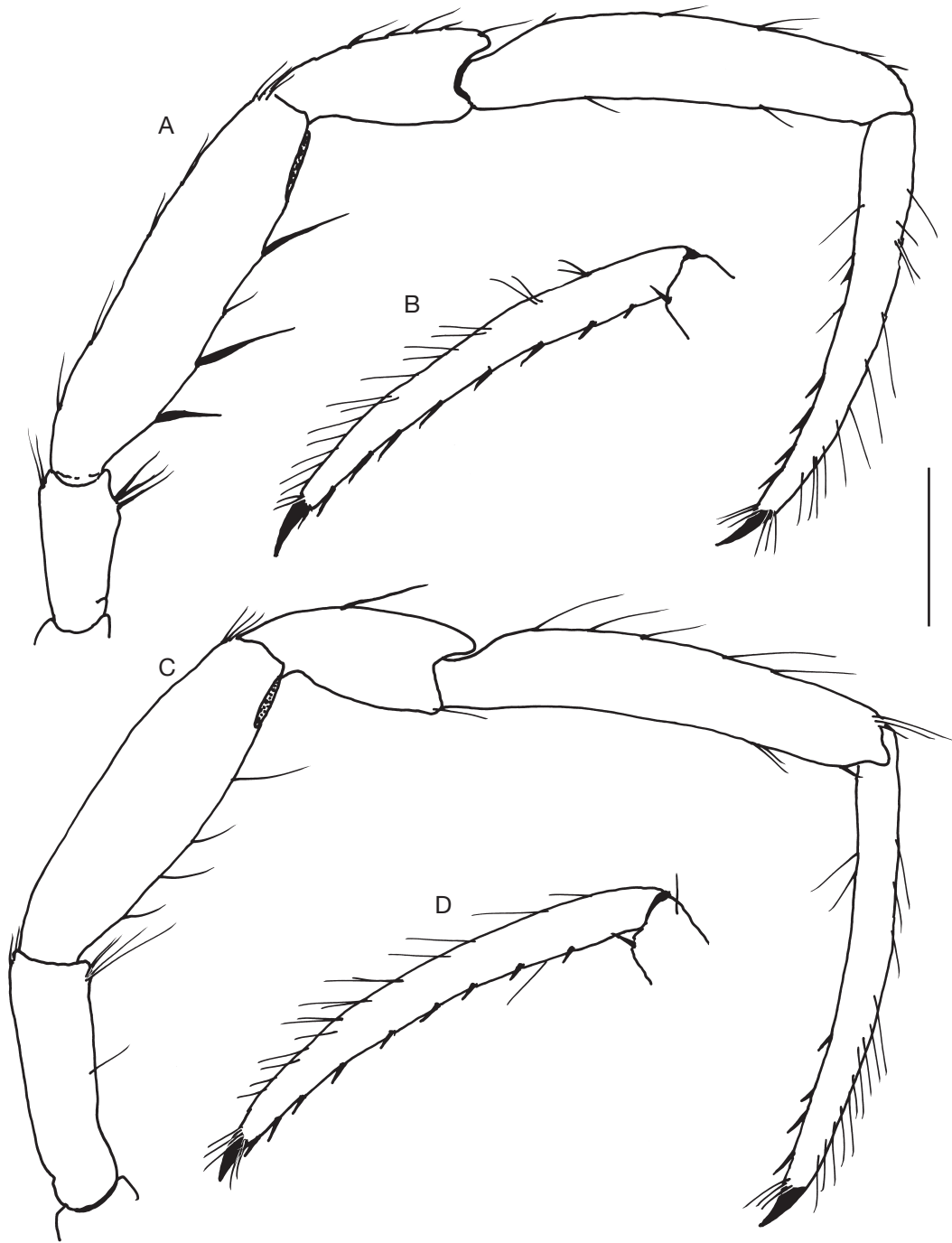


FIG. 3. — *Leptopagurus rhabdodus* n. gen., n. sp., holotype ♂ 1.1 mm, Curaçao, USNM 1297635: **A**, right pereopod 2, lateral view; **B**, dactyl of same, mesial view; **C**, right pereopod 3, lateral view; **D**, dactyl of same, mesial view. Scale bar: 0.3 mm.

*Left cheliped (Fig. 2D-F)*

Narrowly elongate, chela glabrous except for sparse short setae; dactyl and fixed finger each terminating in sharp corneous claw slightly overlapping when closed, cutting edges consisting of row of mostly fused minute corneous teeth. Dactyl about as long as palm; dorsal and ventral surfaces rounded. Palm dorsal surface with weakly raised longitudinal median ridge armed with minute tubercles; ventral surface convex, smooth. Carpus about as long as merus; dorsal surface nearly

flat, dorsodistal margin unarmed; dorsomesial margin with several long capsulate setae proximally and sparse setae distally; dorsolateral margin with row of tufts of short setae; ventral surface convex. Merus subtriangular in cross-section; dorsal margin with row of short tufts of setae; ventral surface with cluster of several long capsulate setae (Fig. 2E, F); ventrolateral and ventromesial margins each with row of small spines. Ischium glabrous. Coxa with row of setae on ventromesial distal angle.



FIG. 4. — *Leptopagurus rhabdotus* n. gen., n. sp.: **A**, Dominica: ♂ 0.9 mm, CURASUB 16-12, USNM 1291967, dorsal view; **B-F**, Curaçao: **B**, ♂ (in shell) 1.5 mm, dorsal view, USNM 1297449 (ULLZ 16921); **C, D**, holotype ♂ 1.1 mm, USNM 1297635 (ULLZ 16890), dorsal (**C**) and right lateral (**D**) views; **E, F**, ♂ 1.0 mm, USNM 1297279, left (**E**) and right (**F**) lateral views.

#### *Ambulatory legs (Fig. 3A-D)*

Long, slender, exceeding tip of chelipeds by about 0.3 length of dactyls when fully extended, sparsely setose. Dactyls each broadly curved, about 1.1 times as long as propodus, terminating in sharp corneous claw; with ventromesial row of eight or nine slender corneous spinules each arranged in small acute angle; with dorsal row of moderately long setae. Propodi each broadly curved, few setae on dorsal and ventral margins, lateral and mesial faces glabrous. Carpi each with blunt dorsodistal angle, few setae on dorsal margin. Meri each somewhat laterally compressed, lateral and mesial faces glabrous, dorsal margin with few long setae; ventral margin with row of several long, well spaced capsulate setae (pereopod 2) or simple setae (pereopod 3). Ischia with capsulate setae on ventrodistal angle (pereopod 2) or simple setae (pereopod 3). Anterior lobe of sternite XI (of pereopods 3; Fig. 1D) subsemicircular, fringe of short setae on distal margin.

#### *Fourth pereopods (Fig. 1E)*

Semichelate. Dactyl weakly curved, terminating in short, inwardly directed corneous claw, lacking preungual process; propodal rasp with single row of ovate corneous scales. Carpus unarmed except for few short setae dorsally. Merus unarmed except for with dorsodistal tuft of long setae.

#### *Fifth pereopods*

Chelate. Propodal rasp extending on dorsal surface for about 0.7 length of propodus.

#### *Uropods and telson (Fig. 1F)*

Uropods markedly asymmetrical, left largest. Telson nearly symmetrical, longer than broad, with distinct lateral indentations; anterior lobes about as long as posterior lobes; posterior lobes with chitinous lateral margins, lobes separated by U-shaped median cleft, terminal margins weakly oblique, each armed with four spines, lateral-most strongest, curving ventrolaterally.

#### *Sexual tubes (Fig. 1G) and pleopods*

Males with coxae of pereopods 5 symmetrical, with short, subequal, stout, membranous sexual tubes (Fig. 1G) curving forward; posterior portion of gonopores each with fringe of setae; with unpaired left pleopods 3-5. Females unknown.

#### *Genetic data*

See Table 1.

#### *Colour (Fig. 4)*

Shield and ocular acicles white. Ocular peduncles orange with broad median white or semi-transparent stripe; corneas dark with white iridescence. Antennular and antennal peduncles light orange on lateral and mesial faces, otherwise semi-transparent white. Chelipeds with dorsal surfaces of chelae light orange except for whitish tone on teeth and cutting edges of dactyl and fixed fingers; meri and carpi each with three light orange stripes on dorsal surfaces. Ambulatory legs semitransparent white; meri, carpi and propodi each with

two light orange stripes on lateral and mesial surfaces, and orange dorsal margins.

#### REMARKS

In addition to generic characters, this minute new species stands out among western Atlantic pagurids by the striking, striped color pattern (Fig. 4). The capsulate setae on the ventral faces of the meri of both chelipeds also provide a distinguishing character, and conceivably these may serve some presently unknown specialized function. Somewhat similar capsulate setae to those found in *Leptopagurus rhabdotus* n. gen., n. sp., have been reported in a number of species of pagurid genera, although not on the ventral faces of the cheliped meri, instead being found on the third through fifth sternites in some species of *Pylopagurus* A. Milne Edwards & Bouvier, 1893, on the lateral and mesial faces of the left cheliped carpus in *Cycetopagurus morgani* McLaughlin, 2004, and on dorsal and mesial surfaces of the carpi of right and left chelipeds *Pseudopagurodes annae* Rahayu & Komai, 2013, and *P. capsellatus* Rahayu & Komai, 2013.

Of the micro-pagurids included in this report, *Leptopagurus rhabdotus* n. gen., n. sp. is the only species that has been found in more than one island locality, being collected in both Curaçao and Dominica.

#### Genus *Nematopaguroides*

Forest & de Saint Laurent, 1968

*Nematopaguroides* Forest & de Saint Laurent, 1968: 156. — Wang & McLaughlin 2000: 957. — McLaughlin 2003: 125.

TYPE SPECIES. — *Nematopaguroides fagei* Forest & de Saint Laurent, 1968, by original designation.

#### REMARKS

Prior to the present description, *Nematopaguroides* included only two species, both distributed in western Atlantic, *N. fagei* Forest & de Saint Laurent, 1968 and *N. pusillus* Forest & de Saint Laurent, 1968.

#### *Nematopaguroides karukera* n. sp.

(Figs 5-8; Table 1)

TYPE MATERIAL. — **Holotype**. ♂ 1.3 mm, Guadeloupe, sta GS 15, off Deshaies, Sec Ferry, 16°17.51'N, 61°48.96'W, 27 m, 12.V.2012, [MNHN-IU-2013-5307](#).

**Paratypes**. Guadeloupe: 1 ♂ 1.2 mm, sta GB 03, 16°21.72'N, 61°36.35'W, 22 m, 5.V.2012, [MNHN-IU-2013-5634](#) (USNM 1292074); 1 ovig ♀ 0.9 mm, sta GD 05, 16°22.61'N, 61°36.33'W, 80 m, 5.V.2012, [MNHN-IU-2013-5636](#); 1 ♂ 1.4 mm, sta GS 07, 16°08.43'N, 61°46.92'W, 12 m, 7.V.2012, [MNHN-IU-2013-5597](#); 1 ♂ 1.3 mm, sta GS 07, [same station data], [MNHN-IU-2013-5596](#); 1 ♀ 1.0 mm, Pointe à Lézard, sta GS 07, [same station data], [MNHN-IU-2013-5598](#); 1 ♂ 1.2 mm, sta GS 07, [same station data], [MNHN-IU-2013-5104](#); 1 ♂ 1.5 mm, 2 ♀ 0.9, 1.0 mm, sta GR 10, 16°08.43'N, 61°46.92'W, 29 m, 7.V.2012, [MNHN-IU-2013-5022](#); 2 ♂ 1.2, 1.5 mm, 2 ♀ 1.0, 1.2 mm, 1 ovig ♀ 1.5 mm, sta GM 11, 1 m, 16°11.97'N, 61°34.28'W, 11.V.2012, [MNHN-IU-2013-4852](#); 1 ♂ 0.9 mm, sta GB 13, 16°23.26'N,

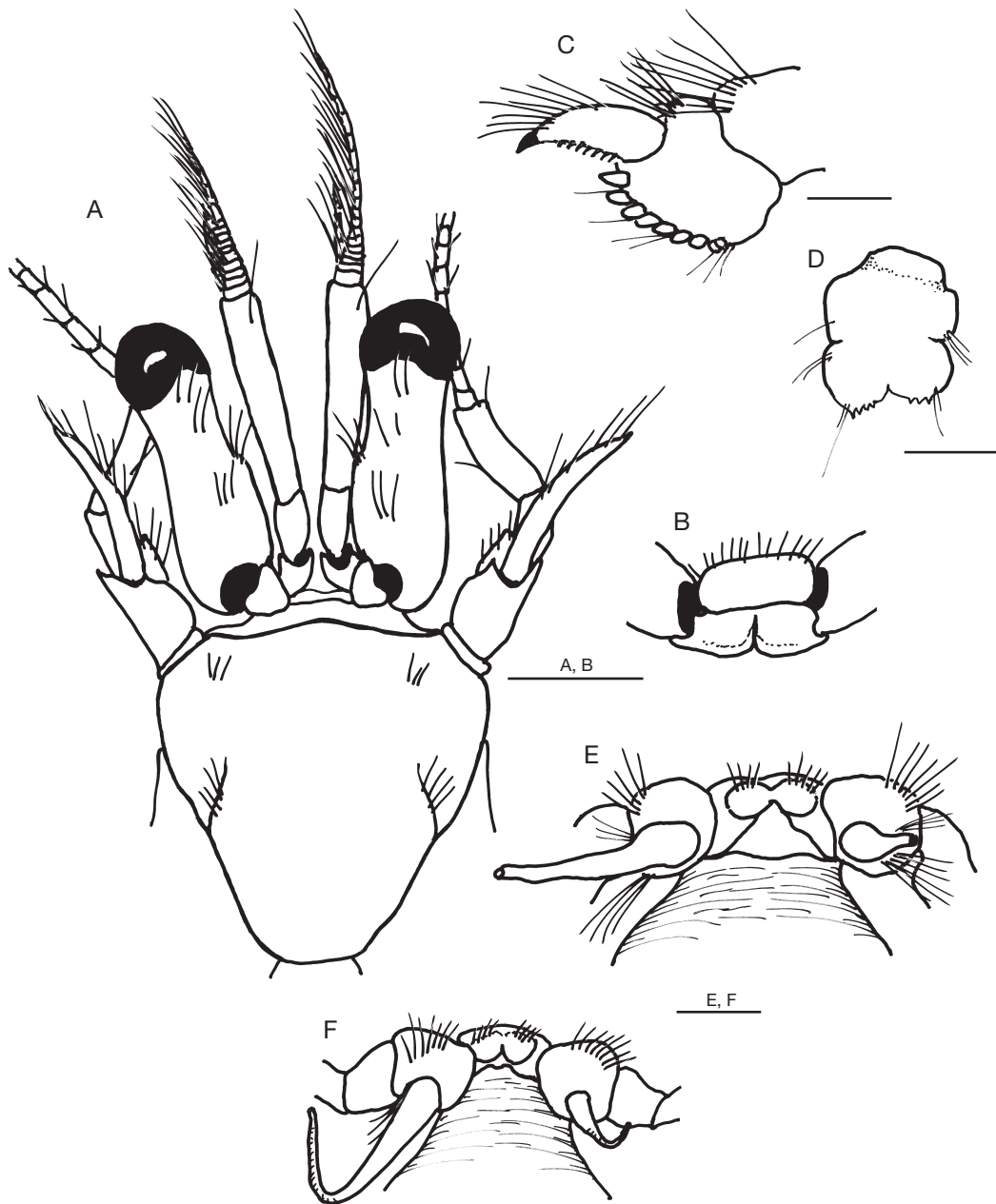


FIG. 5. — *Nematopaguroides karukera* n. sp., Guadeloupe: **A, C-E**: holotype ♂ 1.3 mm, sta GS 15, [MNHN-IU-2013-5307](#); **B**, paratype ♂ 1.5 mm, sta GM 11, [MNHN-IU-2013-4852](#); **F**, paratype ♂ 1.4 mm, sta GS 07, [MNHN-IU-2013-5597](#); **A**, shield and cephalic appendages, dorsal view; **B**, sternite XI of third pereopods, ventral; **C**, propodus and dactyl of left fourth pereopod, lateral view; **D**, telson, dorsal view; **E, F**, sternite XIII and coxae of fifth pereopods with sexual tubes, ventral view. Scale bars: A, B, 0.5 mm; C-F, 0.25 mm.

61°31.79'W, 10 m, 14.V.2012, [MNHN-IU-2013-5480](#); 1 ♂ 1.5 mm, sta GS 13, 16°02.4'N, 61°45.6'W, 50 m, 11.V.2012, [MNHN-IU-2013-5252](#); 1 ovig ♀ 1.2 mm, sta GS 15, [same station data as holotype], [MNHN-IU-2013-5450](#) (USNM 1292075); 1 ♀ 1.0 mm, sta GB 16, 16°27.34'N, 61°32.07'W, 27 m, 16.V.2012, [MNHN-IU-2013-5618](#) (USNM 1292076); 1 ♂ 1.5 mm, 1 ovig ♀ 1.2 mm, sta GD 17, 16°12.55'N, 61°47.12'W, 30 m, 12.V.2012, [MNHN-IU-2013-5629](#) (USNM 1292077); 4 ♂ 0.7-1.5 mm, 1 ♀ 1.0 mm, sta GS 18, 16°23.74'N, 61°32.07'W, 49 m, 15.V.2012, [MNHN-IU-2013-5233](#); 1 ♂ 1.2 mm, sta GB 19, 16°23.26'N, 61°31.79'W, 11 m, 17.V.2012, [MNHN-IU-2013-5130](#); 2 ♂ 0.7, 1.2 mm,

sta GS 19, 16°23.26'N, 61°31.79'W, 11 m, 17.V.2012, [MNHN-IU-2013-5254](#); 1 ♂ 1.3 mm, sta GS 20, 16°27.34'N, 61°32.07'W, 19 m, 16.V.2012, [MNHN-IU-2013-5453](#); 1 ♂ 1.2 mm, sta GS 21, 16°23.26'N, 61°31.79'W, 14 m, 16.V.2012, [MNHN-IU-2013-4407](#); 1 ovig ♀ 1.0 mm, sta GB 30, 16°10.97'N, 61°32.41'W, 16 m, 25.V.2012, [MNHN-IU-2013-5318](#).

ETYMOLOGY. — The species name “karukera” is that used by the Caribs or original inhabitants of the island currently known as Guadeloupe, where this new species was discovered. The Carib name roughly means “island with beautiful waters.”

**DISTRIBUTION.** — So far known only from the Caribbean island of Guadeloupe. Depth: 1-80 m.

**HABITAT.** — Found in gastropod shells.

#### DESCRIPTION

##### *Gills and shield (Fig. 5A)*

Eleven pairs of biserial phyllobranch gills. Shield (Fig. 5A) about as long as broad; anterior margin between rostrum and lateral projections weakly concave; anterolateral margins sloping or weakly terraced; posterior margin roundly truncate; dorsal surface smooth except for short row of tufts of setae anteriorly on either side of midline, and oblique row beginning at about midpoint of each lateral margin. Rostrum broadly rounded to obsolete. Lateral projections broadly subtriangular, terminating bluntly or with minute spine.

##### *Ocular peduncles*

About 0.8 length of shield; dorsal surfaces each with row of sparse tufts of short stiff setae, mesial surface of each peduncle with low knob bearing short stiff setae; corneas moderately dilated. Ocular acicles small, subtriangular, with concave dorsal surface; terminating bluntly and with small submarginal spine.

##### *Antennular peduncles*

Moderately long, exceeding distal margins of cornea when fully extended by about 0.3 length of ultimate segments. Ultimate segment nearly naked except for one or two long dorsodistal setae. Penultimate and basal segments naked.

##### *Antennal peduncles*

Slightly exceeding distal margins of corneas when fully extended. Fifth through third segments with scattered setae. Third segment with sparse tuft of stiff setae on blunt ventrodistal angle. Second segment sparsely setose; with dorsolateral distal angle produced into short spine-like process not quite reaching proximal margin of fourth segment; dorsomesial distal angle with short spine. First segment unarmed. Antennal acicle relatively short, reaching to about midline of cornea, broadly curving outward and terminating in strong spine, mesial margin with tufts of setae. Flagella long, overreaching tip of right cheliped; with few setae 1-2 flagellar articles in length and spaced every three or four flagellar articles.

##### *Mouthparts (Fig. 6A-G)*

Mandible (Fig. 6A) with 3-segmented palp. Maxillule (Fig. 6B) with internal lobe of endopod weakly produced, external lobe with long seta distally. Maxilla (Fig. 6C) with endopod slender, slightly shorter than distal lobe of basal endite but overreaching distal margin of scaphognathite. First maxilliped (Fig. 6D) with slender endopod, exopod with narrow proximal segment and thick flagellum. Second maxilliped (Fig. 6E) without distinguishing characters. Third maxilliped (Fig. 6F, G) with ischium armed basally with small spine; crista dentata weak, bearing about eight small subequal teeth in addition to two longer slender teeth distally, one strong accessory tooth.

##### *Right cheliped (Fig. 7A, B)*

Chelipeds not much different in length, right stouter. Right cheliped with sparse setae often arranged in tufts. Dactyl 0.7-0.8 length of palm, cutting edge with two or three widely-spaced, unequal, blunt calcareous teeth, row of minute corneous teeth distally, and terminating in small corneous claw slightly overlapped by tip of fixed finger; surfaces unarmed except for sparse setae and minute tubercle on mesial margin proximally. Fixed finger similar to dactyl, often slightly overreaching tip of dactyl. Palm about 1.2 times as long as carpus, dorsally unarmed except for sparse setae and row of small spines on dorsolateral and dorsomesial margins; ventral surface convex, nearly glabrous. Carpus about as long as merus; dorsal surface weakly convex, dorsodistal margin with small median spine; dorsolateral and dorsomesial margins each with somewhat irregular row of well spaced spines; lateral face rounded, mesial face flat, vertical; ventral surface rounded and with sparse setae. Merus subtriangular; dorsal, lateral and mesial surfaces with short transverse rows of tufts of setae, dorsodistal margin with small median spine; ventrolateral margin with small spine distally; ventral surface with distal row of setae and small distal spine. Ischium sparsely setose. Coxa unarmed except for row of setae on ventromesial distal angle.

##### *Left cheliped (Fig. 7C, D)*

Reaching nearly to tip of fingers of right cheliped, moderately slender, similar to right in setation. Dactyl and fixed finger terminating in sharp, inwardly curved corneous claw slightly overlapping when close; surfaces with sparse setae; dactyl 1.2 times as long as palm; cutting edges with minute calcareous teeth and row of closely set corneous spinules on distal 0.75. Palm about 0.5 as long as carpus, dorsal surface with median, longitudinal row of minute well-spaced spines; lateral and mesial faces rounded, sparsely setose; ventral surface convex, unarmed except for sparse setae. Carpus slightly shorter to about as long as merus; dorsal surface somewhat flat, with dorsolateral and dorsomesial row of well spaced small spines; ventral surface convex, sparsely setose. Merus subtriangular; dorsal, lateral and mesial surfaces with short transverse rows of tufts of setae, dorsodistal margin with or without small median spine; ventrolateral margin with row of four or five spines, ventromesial margin with small distal spine. Ischium sparsely setose. Coxa unarmed except for row of setae on ventromesial distal angle.

##### *Ambulatory legs (Fig. 8A, B)*

Exceeding tip of right cheliped by about 0.2-0.5 length of dactyls (exceeding right cheliped more in females than in males), dorsal and ventral margins of meri, carpi and propodi with well-spaced low knobs bearing long setae. Dactyls straight except for inwardly curved distal portion with sharp corneous claw, 1.3-1.6 as long as propodus, with ventromesial row of 5-7 long and slender corneous spinules; dorsal and ventral margins with few long setae. Propodi nearly straight, 1.3-1.7 as long as carpus; with scattered setae on lateral and mesial faces. Carpi usually each with small dorsodistal spine.

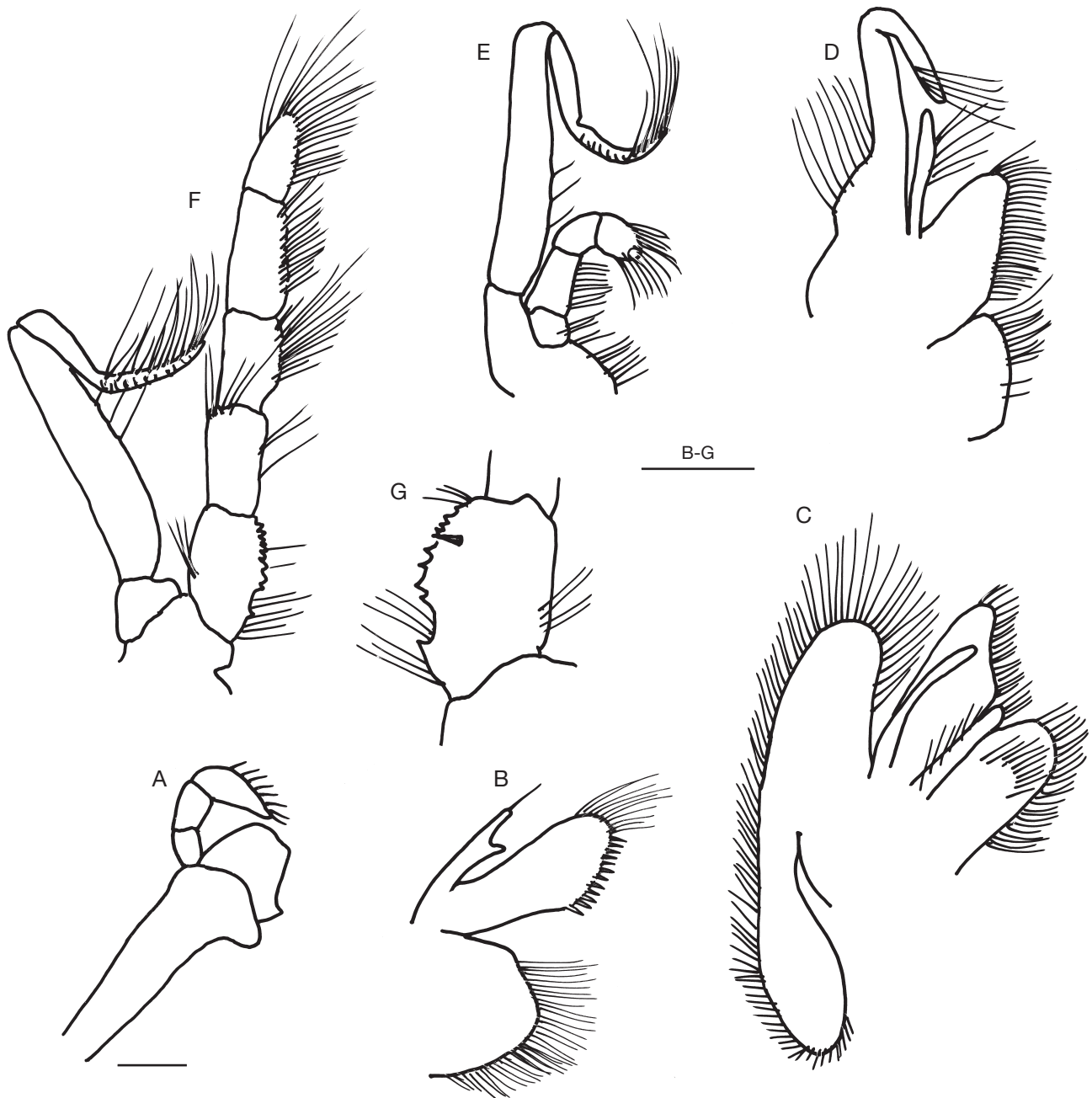


FIG. 6. — *Nematopaguroides karukera* n. sp., holotype ♂ 1.3 mm, Guadeloupe, sta GS 15, MNHN-IU-2013-5307: left mouthparts, internal view: **A**, mandible; **B**, maxillule; **C**, maxilla; **D**, first maxilliped; **E**, second maxilliped; **F**, third maxilliped; **G**, ischium of same. Scale bars: 0.2 mm.

Meri somewhat laterally compressed, lateral and mesial faces naked or with scattered short setae. Ischia with long setae on dorsal and ventral margins. Anterior lobe of sternite XI (of pereopods 3; Fig. 5B) subsemicircular or subrectangular, with fringe of setae on distal margin.

#### *Fourth pereopods (Fig. 5C)*

Semichelate. Dactyl terminating in short, inwardly directed corneous claw, lacking preungual process; propodal rasp with single row of rounded scales. Carpus unarmed except for long setae dorsally. Merus unarmed except for long dorsodistal setae.

#### *Fifth pereopods*

Chelate. Propodal rasp occupying about one-third of distal surface of lateral face.

#### *Telson (Fig. 5D)*

With distinct transverse lateral indentations; anterior lobes longer than posterior lobes, with few setae; posterior lobes nearly symmetrical, separated by broad and moderately deep median V-shaped cleft; terminal margins slightly oblique, with few setae, each with two or three small spines, usually a more prominent ventrally curved spine at lateral angle; lateral margins slightly rounded or nearly straight.

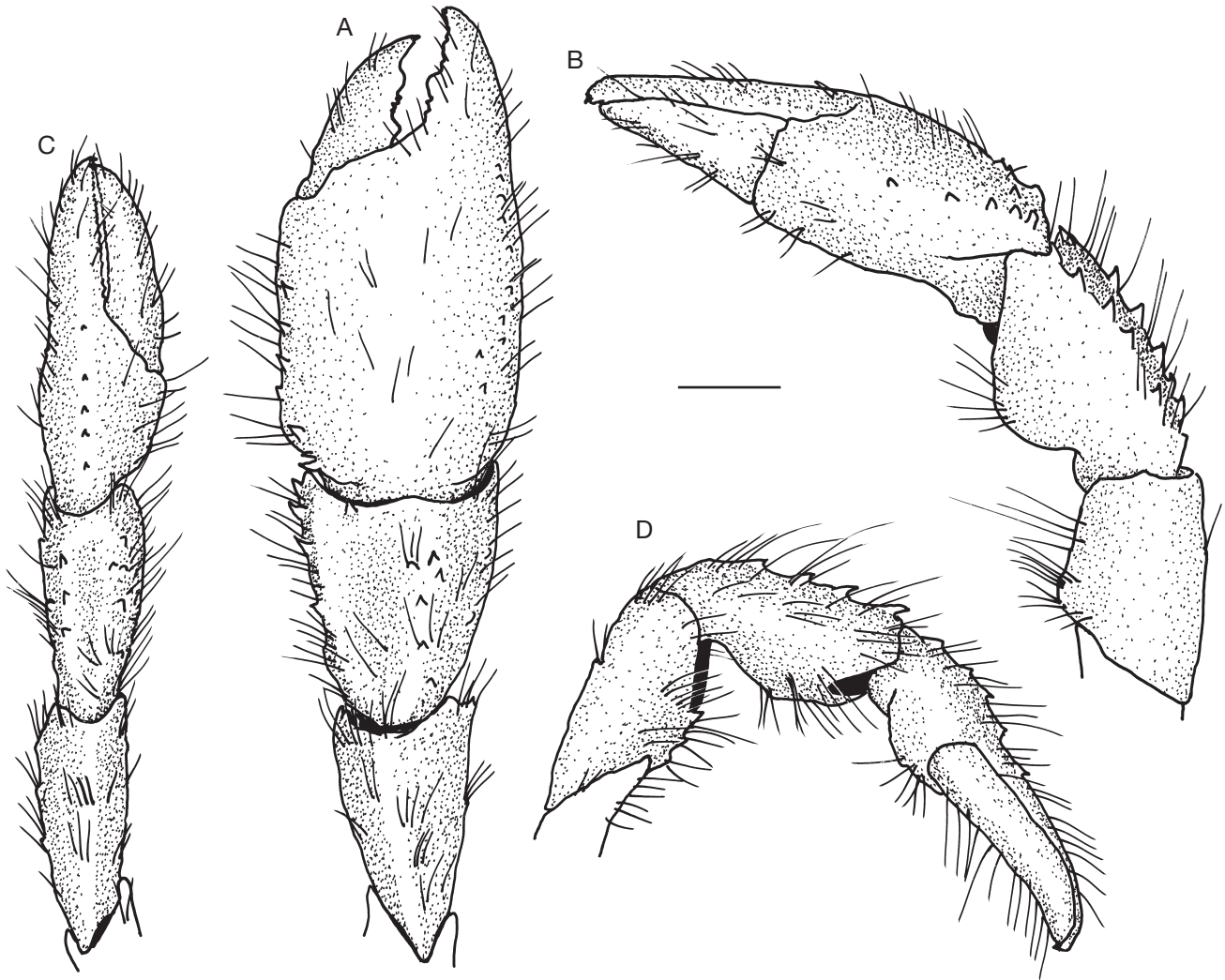


FIG. 7. — *Nematopaguroides karukera* n. sp., holotype ♂ 1.3 mm, Guadeloupe, sta GS 15, MNHN-IU-2013-5307: **A**, right cheliped, dorsal view; **B**, same, mesial view; **C**, left cheliped, dorsal view; **D**, same mesial view. Scale bar: 0.5 mm.

#### *Sexual tubes (Fig. 5E, F) and pleopods*

Males with long, often coiled, and distally filiform sexual tube produced from right coxa of pereopod 5, filiform portion often translucent and invisible except under high magnification; with short, conical sexual tube not distally filiform, produced from coxa of left pereopod 5. Females with pleopods 2-4 ovigerous, with few and relatively large eggs 0.3 mm in maximum width and ranging about 5-8 per pleopod; pleopod 5 not ovigerous, with reduced internal ramus.

#### *Genetic data*

See Table 1.

#### *Colour*

Unknown.

#### REMARKS

As for other species described in this report, individuals of *Nematopaguroides karukera* n. sp. are minute, ranging in size

from 0.9-1.5 mm in shield length, and live in cryptic habitats of corals, rocks, or seagrasses (*Thalassia*, *Halophila*) near corals, where they appear to be abundant (28 specimens were collected). In some males the distal, filamentous portions of the sexual tubes on both sides are so delicate that they are easily broken off during processing, or can be completely transparent and easily overlooked.

When McLaughlin & Rahayu (2007b) transferred *Nematopaguroides reconditus* Wang & McLaughlin, 2000 to *Pseudopagurodes* McLaughlin, 1997, they discussed the morphological differences between species of *Nematopaguroides* and *Pseudopagurodes* and evaluated the morphological justification to keep the two genera separate. They concluded that there is enough morphological evidence to justify the recognition of both genera. *Nematopaguroides fagei*, *N. pusillus*, and this new species indeed are sufficiently similar in morphology and geographic distribution (all three occur only in the western Atlantic) to support McLaughlin & Rahayu's conclusion.

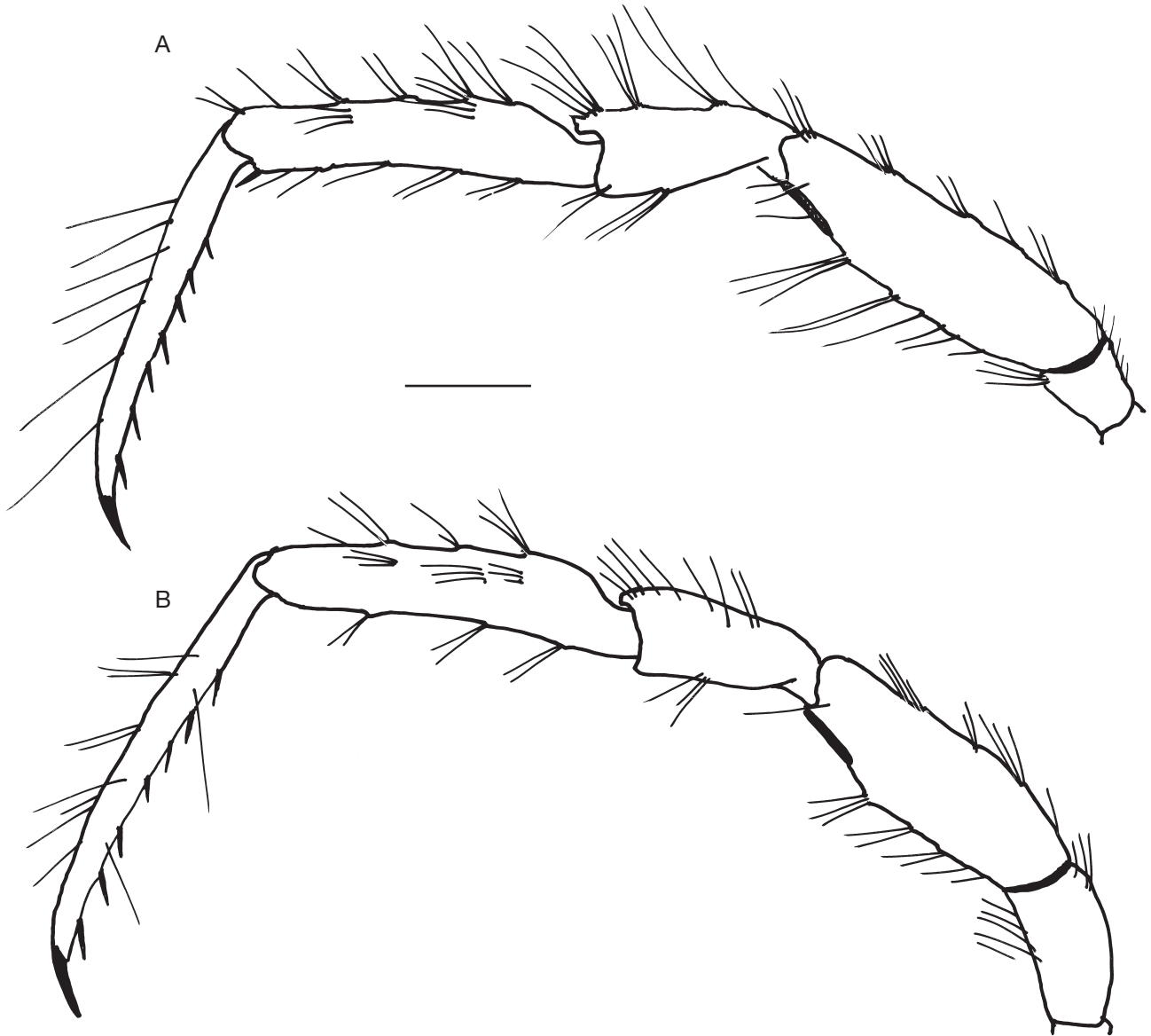


FIG. 8. — *Nematopaguroides karukera* n. sp., holotype ♂ 1.3 mm, Guadeloupe, sta GS 15, MNHN-IU-2013-5307: **A**, left pereopod 2, lateral view; **B**, left pereopod 3, lateral view. Scale bar: 0.5 mm.

*Nematopaguroides karukera* n. sp. is most similar to *N. pusillus*, a western Atlantic species that rarely has been reported (Lemaitre & Tavares 2015). The two can be differentiated by the shape of the rostrum (nearly obsolete in the new species vs obtusely triangular in *N. pusillus*); the setation of ocular peduncles and pereopods 2 and 3 (low knobs with setae on mesial face of ocular peduncle and dorsal and ventral margins of meri, carpi and propodi of pereopods 2 and 3 in the new species vs lacking knobs in *N. pusillus*); length and shape of dactyls of pereopods 2 and 3 (straight and about 1.3 times as long as propodi in the new species vs broadly curved and short, about 1.1 times as long as propodi in *N. pusillus*).

*Nematopaguroides karukera* n. sp. can be separated from *N. fagei* by the shape and spination of the ventral margins of the dactyls of pereopods 2 and 3 (straight and with long spinules arranged at 45° angle in the new species vs broadly

curved and with short spinules appressed against ventral margins or at most arranged at distinctly less than 45° in *N. fagei*); the setose knobs on ocular peduncle and pereopods 2 and 3 (setation without knobs in *N. fagei*); and armature of terminal margins of the posterior lobes of the telson (with weak spines in the new species vs strong, often curved spines in *N. fagei*).

#### Genus *Pagurellus* n. gen.

TYPE SPECIES. — *Pagurellus jenniferae* n. gen., n. sp., by present designation. Gender: masculine.

ETYMOLOGY. — The generic name is derived from the genus name *Pagurus*, combined with the masculine Latin suffix *-ellus* which

denotes something diminutive, in reference to the minute size of specimens in the single species of this new genus.

**DIAGNOSIS.** — Nine pairs of biserial phyllobranch gills, no pleuro-branches on somites X, XI (thoracomeres 5 and 6, above pereopods 2 and 3). Rostrum broadly triangular. Crista dentata with accessory tooth. Chelipeds unequal, right largest and stronger than left. Sternite of somite XI (thoracomere 6, pereopod 3) with semi-circular anterior lobe. Pereopod 4 with single row of scales on propodal rasp, dactyl lacking preungual process. Pereopod 5 semi-chelate. Male with paired, unequal, basally weakly calcified, and distally filamentous sexual tubes on coxae of pereopods 5, left tube longer than right, distally coiled; with unpaired, left pleopods 3-5. Female with paired gonopores. Telson nearly symmetrical, with lateral indentations; terminal margins armed with spines.

**DISTRIBUTION.** — Known based on the type species found in Curaçao. Depth: 224-246.5 m.

#### REMARKS

This new genus is unique in having the combination of nine pairs of biserial gills, narrowly elongate paired (filament like, often distally semitransparent) tubes on both coxae in the male, no preungual process on pereopod 4, and a cryptic habitat. Of all the pagurid genera in which males have sexual tubes, only five have paired tubes with the left being the largest, as in this new genus. However, the number and type of gills in these five genera vary in number from 9 (*Enneobranchus*) to 11 pairs (all others); the gills are biserial in *Anapagurus* Henderson, 1886, and *Pumilopagurus*, and quadriserial in all others.

*Pagurellus* n. gen is most similar, at least superficially, to *Pumilopagurus* McLaughlin & Rahayu, 2008b, in morphology of shield, ocular acicles, ambulatory legs, propodal rasp of pereopod 4, sexual tubes, and telson. However, gill number is different (9 pairs vs 11 pairs in *Pumilopagurus*); the right sexual tube in *Pagurellus* n. gen. is long, and filamentous distally, whereas in *Pumilopagurus* it is short and stout; the chelipeds in *Pagurellus* n. gen. are not as strongly unequal, and the right is not as massive, as in *Pumilopagurus*. Females of *Pagurellus* have paired gonopores, whereas females of *Pumilopagurus* have a single left gonopore.

There is an eerie similarity of the chelipeds of the single species of *Pagurellus* n. gen. with those in species of *Anapagrides* (e.g., *A. reesei* [McLaughlin, 1986]), but otherwise the two genera are markedly different, primarily differing in characters such as gill number (9 pairs vs 11 pairs in *Anapagrides*), ocular acicles (bifid vs simple in *Anapagrides*), preungual process (absent vs present in *Anapagrides*), and male sexual tubes (filamentous, left longest vs stout, right longest in *Anapagrides*).

#### *Pagurellus jenniferae* n. sp. (Figs 9-12; Table 1)

**TYPE MATERIAL.** — **Holotype.** 1 ♂ 1.3 mm, Curaçao, CURASUB 15-06, 246.5 m, in gastropod shell inside bottle, USNM 1267546. **Paratypes.** Curaçao: 1 ovig ♀ 0.9 mm (missing chelipeds), ARMS 14, 224 m, 15.IX.2015, BCURA 0670, USNM 1291918; 1 ovig ♀ 1.0 mm, ARMS 14, [same sta data], BCURA 0704, USNM 1297462; 1 ♂ 1.5 mm, ARMS 14, [same sta data], BCURA 0669, USNM

1297636 (ULLZ 16891); 1 ovig ♀ 0.9, ARMS 14, [same sta data], BCURA 0671, USNM 1291920; 1 ovig ♀ 1.3 mm, ARMS 14, [same sta data], BCURA 0672, USNM 1291922; 1 ovig ♀, 0.7 mm, ARMS 17, 224 m, 15.IX.2015, BCURA 0966, [MNHN-IU-2013-5564](#) (ex USNM 1297507); 1 ovig ♀ 1.1 mm, ARMS 17, [same depth, date], BCURA 0951, [MNHN-IU-2013-5565](#) (ex USNM 1297511); 1 ♂ 1.0 mm, BCURA ARMS 17, [same sta data], BCURA 0964, [MNHN-IU-2013-5566](#) (ex USNM 1297505); 1 ♂ 0.7 mm, ARMS 17, [same sta data], BCURA 0960, USNM 1297501; 1 ♀ 0.9 mm, ARMS 22, 224 m, 15.IX.2015, BCURA 1500, USNM 1297446 (ULLZ 16923); 1 ovig ♀ (damaged, incomplete), ARMS 22, [same sta data], BCURA 1501, USNM 1291921.

**ETYMOLOGY.** — The specific name is designated for Jennifer M. Felder, who has provided us dedicated field and lab assistance on a number of cruises and expeditions over the last decade. Her sharp eye during Curaçao-based DROP and ARMS sampling called our attention to numerous very small paguroid specimens, including a number of those treated in the present paper.

**DISTRIBUTION.** — So far known only from Curaçao, where it was discovered living in ARMS and inside an empty glass bottle. Depth: 224-246.5 m.

**HABITAT.** — Found living in gastropod shells.

#### DESCRIPTION

##### *Shield* (Fig. 9)

Glabrous, about as long as broad; anterior margin between rostrum and lateral projections concave; anterolateral margins sloping; posterior margin roundly truncate. Rostrum broadly rounded, subtriangular, reaching distally to about same level of lateral projections. Lateral projections subtriangular, terminating in small sharp spine, mesial margin rounded and somewhat produced anteriorly as shoulder.

##### *Ocular peduncles*

Relatively short and stout, about 0.7 length of shield; dorsal surfaces naked except for median tuft of short setae; corneas weakly dilated. Ocular acicles subtriangular, dorsal surface flat; terminating in bifid spine.

##### *Antennular peduncles*

Exceeding distal margins of cornea when fully extended by about 0.5 length of ultimate segment. Ultimate segment naked except for one long dorsodistal seta. Penultimate and basal segments naked; basal segment with blunt ventromesial distal angle, and small spine on lateral face.

##### *Antennal peduncles*

Exceeding distal margins of corneas when fully extended by about 0.3 length of fifth segment. Fifth and fourth segments unarmed except for scattered short setae. Third segment with strong spine on ventrodistal angle. Second segment with dorsolateral distal angle produced into spine-like process; dorsomesial distal angle with small spine. First segment unarmed. Antennal acicle reaching to about proximal margin of cornea, broadly curving outward, terminating in strong spine, mesial margin with few short setae. Flagellum slightly exceeding distal margin of right cheliped when extended, with setae < 1-2 flagellar articles in length.

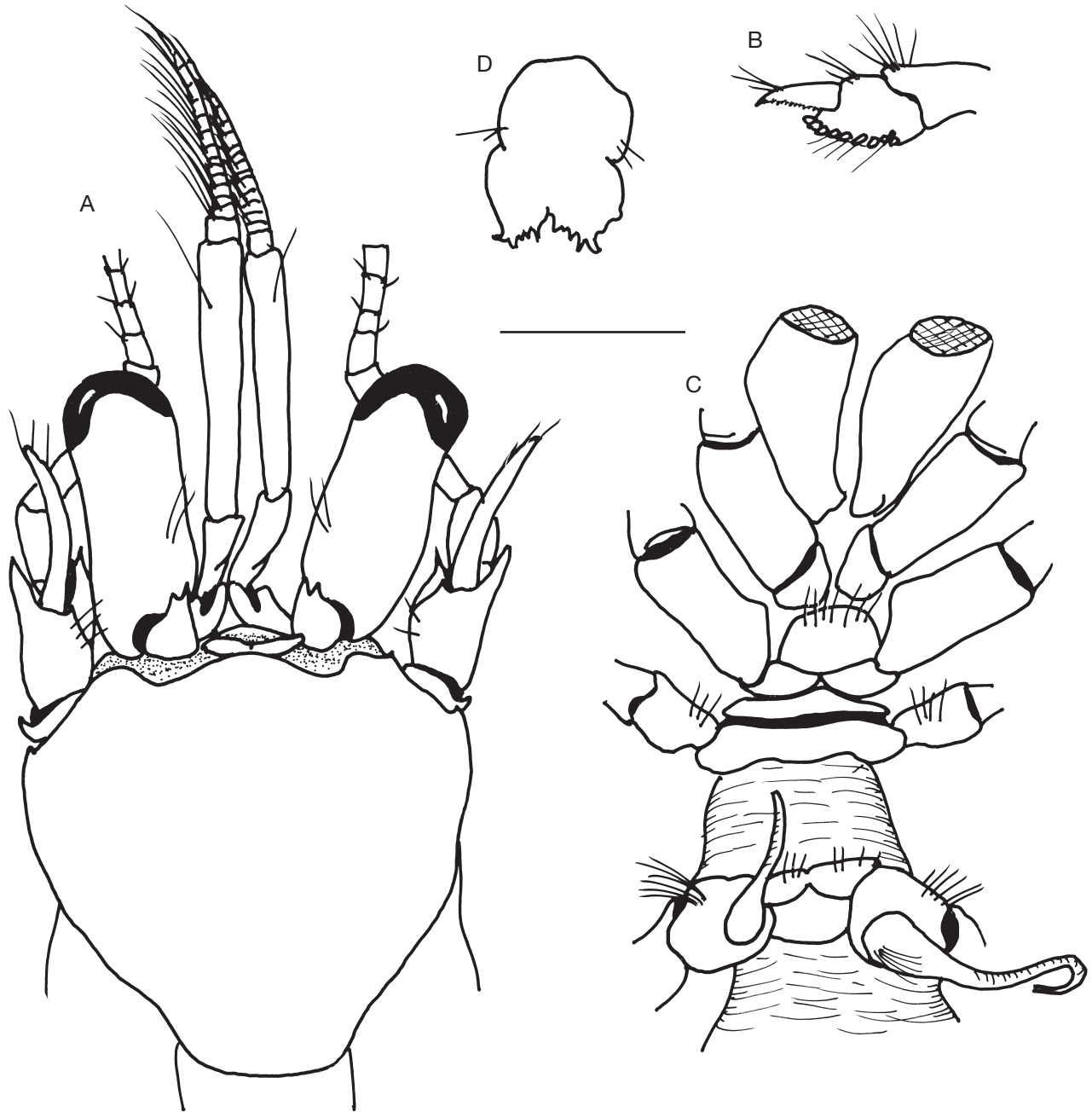


FIG. 9. — *Pagurellus jenniferae* n. gen., n. sp., holotype ♂ 1.3 mm, Curaçao, CURASUB 15-06, USNM 1267546: **A**, shield and cephalic appendages, dorsal view; **B**, propodus and dactyl of left fourth pereopod, lateral view; **C**, sternites IX-XIII, coxae of chelipeds and pereopods 2-5, and sexual tubes, ventral view; **D**, telson, dorsal view. Scale bar: 0.5 mm.

#### *Mouthparts*

Mandible, maxillule, and maxilla not dissected. First maxilliped with slender endopod not exceeding distal endite. Second maxilliped without distinguishing characters. Third maxilliped ischium with crista dentata consisting of about 14 small, subequal teeth, and small accessory tooth.

#### *Right cheliped (Fig. 10A-C)*

Chelipeds unequal, right distinctly longer and stronger than left. Right cheliped moderately elongated, with sparse setae or tufts of setae. Chela about twice as long as broad, dactyl

and fixed finger each terminating in small corneous claw slightly overlapping when closed. Dactyl about 0.7 times as long as palm, unarmed dorsally and ventrally; dorsolateral margin defined by weak rounded ridge; dorsal surface with moderately raised longitudinal median ridge; cutting edge with three large, rounded calcareous teeth, and row of fused small teeth distally. Fixed finger with scattered small spines dorsoproximally; dorsal surface with moderately raised longitudinal median ridge; dorsolateral margin well defined by often sharp ridge continued for half or more of palm; cutting edge with one large rounded calcareous tooth medially, and row

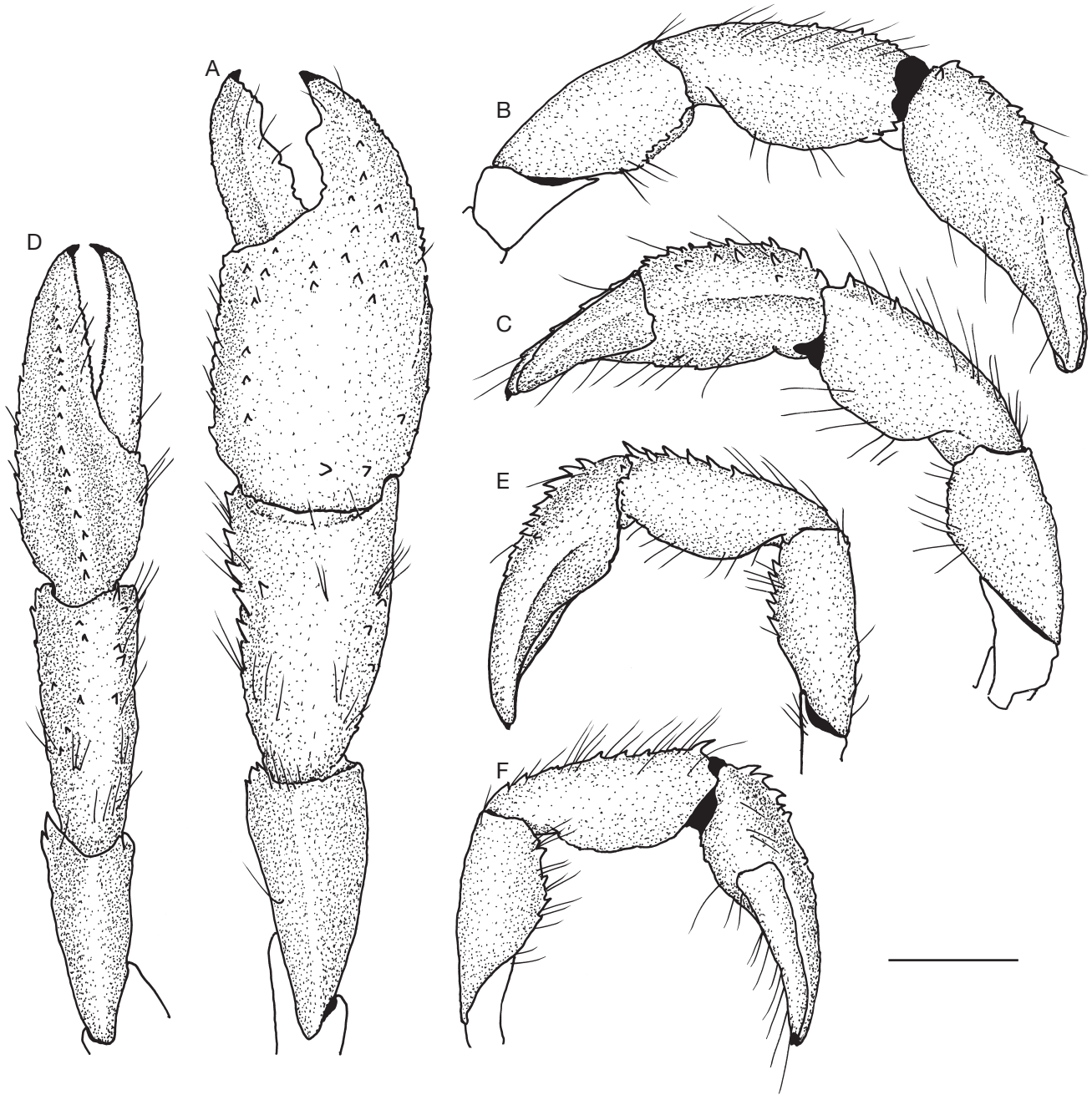


FIG. 10. — *Pagurellus jenniferae* n. gen., n. sp., holotype ♂ 1.3 mm, Curaçao, CURASUB 15-06, USNM 1267546: **A-C**, right cheliped, dorsal view (**A**), lateral view (**B**), mesial view (**C**); **D-F**, left cheliped, dorsal view (**D**), lateral view (**E**), mesial view (**F**). Scale bar: 0.5 mm.

of minute, fused corneous teeth distally. Palm approximately as long as carpus, dorsally convex; dorsal surface with small, well-spaced spines distally, dorsomesial row of small spines, and two or three spines proximally; ventral surface convex, unarmed except for scattered short setae. Carpus about as long as merus; dorsal surface weakly convex, with few scattered small spines; dorsodistal margin unarmed; dorsomesial margin with row of five spines; lateral face rounded, with few scattered small, blunt spines; mesial face flat, nearly vertical; ventral surface convex. Merus subtriangular, distal margin with few short setae; ventrolateral and ventromesial margins

with row of minute spines. Ischium unarmed. Coxa with row of setae on ventromesial distal angle.

#### *Left cheliped (Fig. 10D-F)*

Moderately slender, sparsely setose; dactyl and fixed finger each terminating in sharp corneous claw slightly overlapping when closed, cutting edges consisting of fused row of minute corneous teeth. Dactyl about 1.4 times as long as palm; dorsal and ventral surfaces rounded. Palm dorsal surface with raised longitudinal median ridge usually armed with single row of small spines continued on fixed finger (occasionally

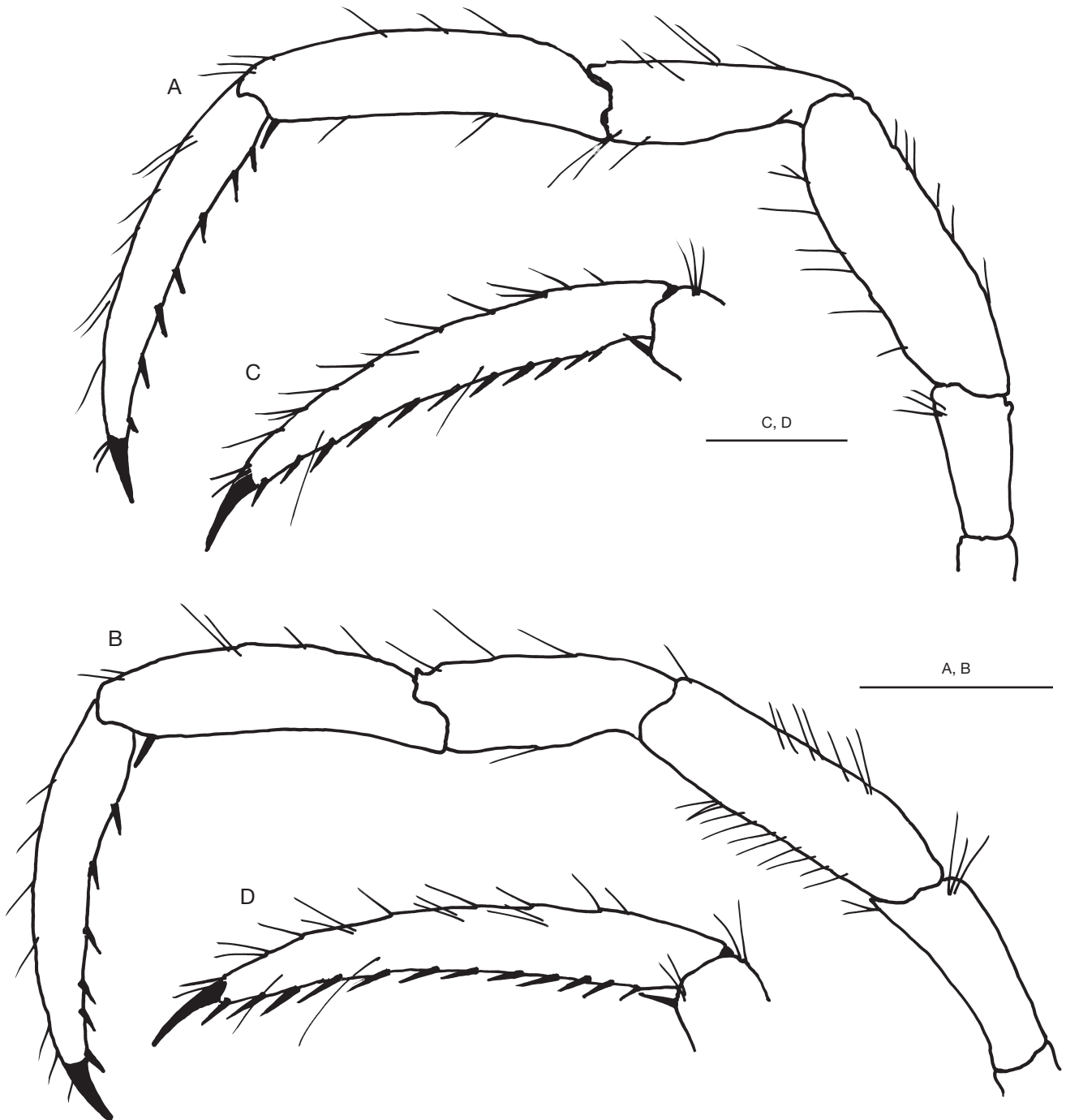


FIG. 11. — *Pagurellus jenniferae* n. gen., n. sp. **A, B**, holotype ♂ 1.3 mm, Curaçao, CURASUB 15-06, USNM 1267546; **C, D**, paratype ♂ 1.5 mm, Curaçao, ARM 14, USNM 1297636: **A**, left pereopod 2, lateral view; **B**, left pereopod 3, lateral view; **C**, dactyl of right pereopod 2, mesial view; **D**, dactyl of pereopod 3, mesial view. Scale bars: 0.5 mm.

with double row of small spines proximally); ventral surface convex, smooth. Carpus about 1.3 times as long as merus; dorsodistal margin with small spine mesially, dorsomesial and dorsolateral margins each with row of few small spines, dorsolateral surface with scattered small spines or tubercles; ventral surface convex, smooth except for sparse setae. Merus unarmed, nearly naked; ventrolateral and ventromesial margins each with row of spines.

#### *Ambulatory legs (Fig. 11A-D)*

Sparsely setose. Dactyl about 1.3 times as long as propodus, broadly curved, terminating in sharp corneous claw, ventromesial margin with row of 6-10 corneous spinules (more numerous in larger specimens  $sl \geq 1.0$  mm) arranged in small acute angles. Propodus nearly straight, about 1.3 times as long as carpus, lacking spines except for slender corneous spinule on ventrodistal angle. Carpus with dorsodistal angle blunt

(pereopod 2) or with small spines (pereopod 3), otherwise unarmed. Merus and ischium unarmed, somewhat laterally compressed. Anterior lobe of sternite XI (of pereopods 3; Fig. 9C) subsemicircular, with fringe of short setae on distal margin.

#### *Fourth pereopods (Fig. 9B)*

Semichelate. Dactyl nearly straight, slender, terminating in short, inwardly directed corneous claw, lacking preungual process; propodal rasp with single row of rounded corneous scales. Carpus unarmed except for few short setae dorsally. Merus unarmed except for with dorsodistal tuft of long setae.

#### *Fifth pereopods*

Chelate. Propodal rasp dorsally extending for about half surface of propodus.

#### *Uropods and telson (Fig. 9D)*

Uropods markedly asymmetrical, left largest, exopods each with row of long bristles dorsodistally. Telson nearly symmetrical, longer than broad, with distinct lateral indentations. Anterior lobes slightly longer than posterior lobes. Posterior lobes nearly symmetrical, separated by narrow, V-shaped median cleft; terminal margins oblique, each armed with row of small spines and strong bifid, ventrolaterally curved spine on posterodistal angle.

#### *Sexual tubes (Fig. 9C) and pleopods*

Males with unequal sexual tubes on coxae of pereopods 5 (Fig. 9C), distally filamentous and often transparent; left tube long, stronger and longer than right, curving laterally and a bit dorsally, coiled distally; right tube short to medium in length, straight, directed obliquely inward; with unpaired left pleopods 3-5. Females with paired gonopores unpaired left pleopods 2-5 (only 2-4 ovigerous), carrying about 20 relatively large eggs about 0.6 in maximum width.

#### *Genetic sequence data*

See Table 1.

#### *Colour (Fig. 12)*

Shield dorsal surface white with light red spots laterally; ocular acicles and second segment of antennal peduncles each with reddish spot on dorsal surface; ocular peduncles with very light reddish band distally, otherwise semi-transparent white. Chelipeds with chelae and carpi very light orange; meri each with short light reddish band or ovate spot distally on dorsolateral and dorsomesial mesial faces. Pereopods 2 and 3 dactyls with two light orange bands (one subdistal, one proximal); propodi each with red band dorsomedially; carpi light orange with whitish dorsal margin; meri with red spot dorsodistally and light orange band medially.

#### REMARKS

The first specimen of this new species was discovered living inside a discarded glass bottle containing numerous minute gastropod shells. Subsequently several additional specimens

were collected in ARMS, where the species seems to find a suitable environment.

### Genus *Pagurina* n. gen.

TYPE SPECIES. — *Pagurina bifida* n. gen., n. sp., by monotypy.

ETYMOLOGY. — The generic name is derived from the genus name *Pagurus*, and using the Latin feminine suffix *-ina*, which denotes something diminutive, in reference to the minute size of specimens in the single species of this new genus.

DISTRIBUTION. — Known only from the type species collected in Guadeloupe, Lesser Antilles, Caribbean Sea, at a depth of 10 m.

DIAGNOSIS. — Nine pairs of biserial phyllobranch gills, no pleuro-branches on somite XII (thoracomere 7, above pereopod 4). Rostrum subtriangular. Ischium with weak crista dentata, lacking accessory tooth. Chelipeds subequal. Sternite of somite XI (thoracomere 6, pereopod 3) with anterior lobe rectangular. Pereopod 4 with single row of scales on propodal rasp, dactyl lacking preungual process. Pereopod 5 semi-chelate. Male with paired gonopores, and unpaired left sexual tube on coxa of pereopods 5; with unpaired, left pleopods 3-5. Female conditions unknown. Telson nearly symmetrical, with lateral indentations; terminal margins oblique.

#### REMARKS

Although superficially *Pagurina* n. gen. might give the appearance that it could be placed in the catch-all genus *Pagurus* Fabricius, 1775, a number of characters clearly indicate that it must be considered a separate genus. The three main characters that place this taxon outside of *Pagurus*, or any other known genus of Paguridae, are the number of gills (nine in *Pagurina* n. gen. vs 11 in most *Pagurus*), the absence of an accessory tooth (present in *Pagurus*) on the crista dentata, and presence of a short sexual tube (lacking in majority of *Pagurus*).

### *Pagurina bifida* n. sp. (Figs 13-15; Table 1)

TYPE MATERIAL. — **Holotype**. ♂ 0.8 mm, Guadeloupe, sta GB 34, Petite-Terre, 16°10.45'N, 61°8.16'W, 10 m, 27.V.2012, MNHN-IU-2013-5643.

ETYMOLOGY. — The specific name is derived from the Latin, using the prefix *bi-*, meaning two or double, and the suffix *-fid*, divided, in reference to bifid condition of the ocular acicles of the holotype of this new species.

DISTRIBUTION. — Known so far only from Guadeloupe, Lesser Antilles, Caribbean. Depth: 10 m.

HABITAT. — Gastropod shells.

#### DESCRIPTION OF HOLOTYPE

##### *Shield (Fig. 13A)*

Glabrous, about as long as broad; anterior margin between rostrum and lateral projections weakly concave; anterolateral margins sloping; posterior margin roundly truncate. Rostrum broadly and bluntly subtriangular, reaching distally to about same level of lateral projections. Lateral projections subtriangular, terminating in small sharp spine.



FIG. 12. — *Pagurellus jenniferae* n. gen., n. sp., Curaçao: **A**, **B**, ♂ 1.5 mm, ARMS 14, USNM 1297636 (ULLZ 16891), dorsal (**A**) and posterolateral (**B**) views; **C**, ♀ (in shell) 0.9 mm, ARMS 22, USNM 1297446 (ULLZ 16922), dorsal view; **D**, ovig ♀ 0.9 mm, USNM 1291918 (ULLZ 16891), right lateral view.

#### *Ocular peduncles*

Relatively short and stout, about 0.7 length of shield; dorsal surfaces naked; corneas weakly dilated. Ocular acicles subtriangular, terminating in bifid spine.

Antennular peduncles exceeding distal margins of cornea when fully extended by about 0.2 length of ultimate segment. Ultimate segment naked except for three or four long dorsodistal setae. Penultimate and basal segments naked; basal segment with blunt ventromesial angle, and small spine on lateral face.

#### *Antennal peduncles*

Reaching to about distal margins of corneas when fully extended. Fifth and fourth segments unarmed except for scattered short setae. Third segment with blunt ventrodistal angle. Second segment with dorsolateral distal angle produced into spine-

like process; dorsomesial distal angle with small spine. First segment unarmed. Antennal acicle relatively short, reaching to about proximal margin of cornea, broadly curving outward, terminating in strong spine with setae, mesial margin with few short setae. Flagella missing in holotype.

#### *Mouthparts (Fig. 13B)*

Mouthparts not dissected. Third maxilliped ischium with weakly dentate (serrate) crista dentata, lacking accessory tooth.

#### *Right cheliped (Fig. 14A-C)*

Chelipeds slightly unequal, right somewhat stronger than left, sparsely setose. Right cheliped moderately elongated. Chela about 2.3 times as long as broad, dactyl and fixed finger each terminating in small corneous claw slightly overlapping when

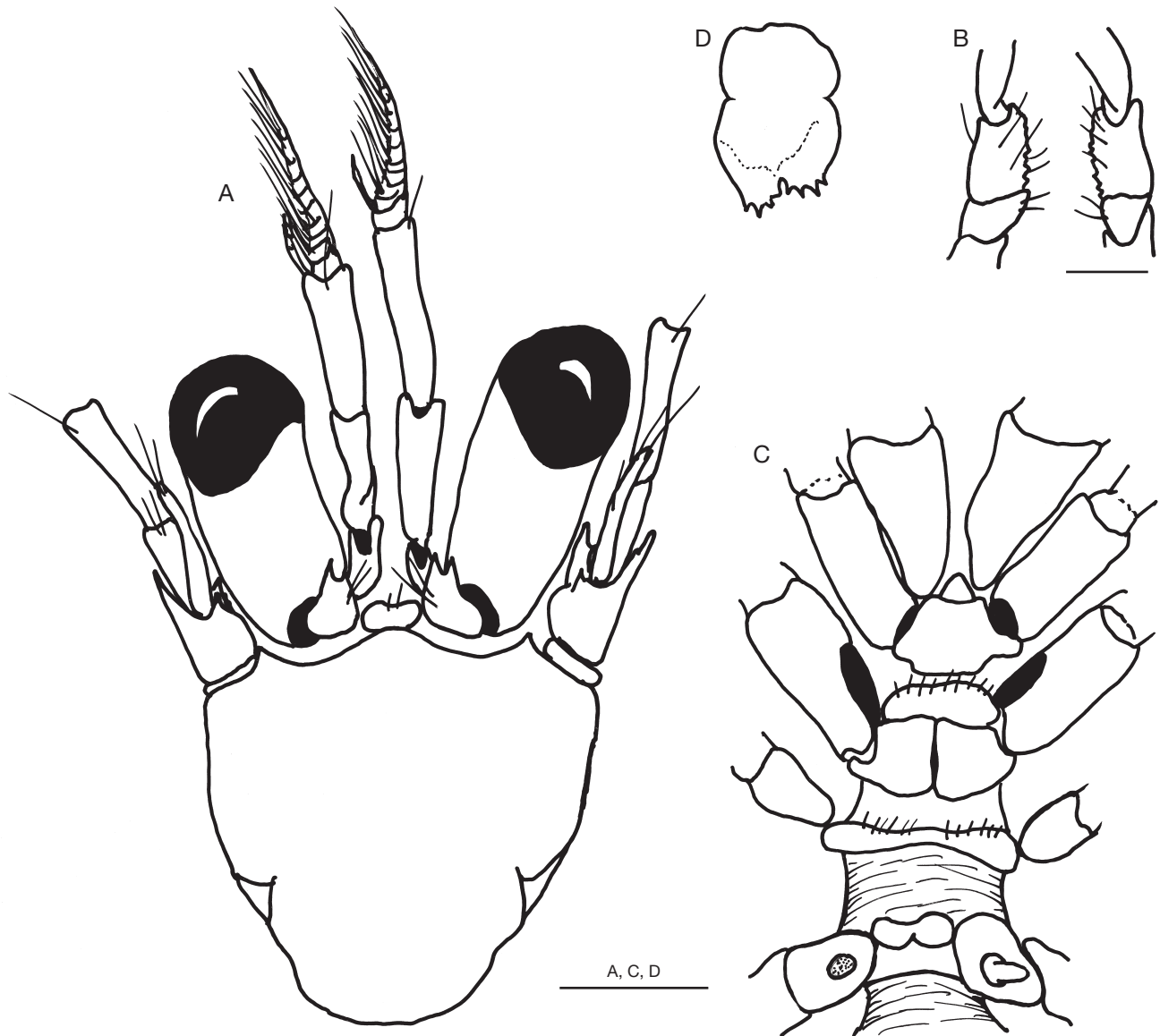


FIG. 13. — *Pagurina bifida* n. gen., n. sp., holotype ♂ 0.8 mm, Guadeloupe, sta GB 34, MNHN-IU-2013-5643: **A**, shield and cephalic appendages, dorsal view; **B**, basis-ischium of left and right third maxillipeds, outer view; **C**, sternites IX-XIII, coxae of chelipeds and pereopods 2-5, and left sexual tube, ventral view; **D**, telson, dorsal view. Scale bars: A, C, D, 0.5 mm; B, 0.2 mm.

closed. Dactyl about 0.7 times as long as palm, unarmed except for two small tubercles on dorsal surface and sparse setae on mesial margin; cutting edge with two large calcareous teeth proximally, and uneven row of small fused and sharp calcareous teeth distally. Fixed finger with scattered setae and row of small, slender spines proximally on dorsolateral margin; cutting edge similar to that of dactyl. Palm approximately as long as carpus, dorsally convex; dorsal surface with median row of low tubercles or small spines; dorsolateral margin with distal row of small, slender, sharp spines obscured by setae; ventral surface convex, glabrous. Carpus with dorsal surface convex, with scattered setae; dorsodistal margin with two small blunt spines; lateral face rounded; dorsomesial margin with row of two sharp spines distally; mesial face flat, nearly vertical; ventral surface convex, glabrous. Merus subtrian-

gular, dorsal margin with few short setae; ventrolateral and ventromesial margins with one or two small, slender spines respectively. Ischium unarmed. Coxa with row of setae on ventromesial distal angle.

#### *Left cheliped (Fig. 14D-F)*

Moderately elongated; dactyl and fixed finger unarmed dorsally except for scattered setae, terminating in sharp corneous claws slightly overlapping when closed, cutting edges consisting of fused row of small calcareous teeth interspersed with fused corneous teeth. Dactyl about as long as palm; dorsal and ventral surfaces rounded. Palm dorsal surface with median row of small tubercles; dorsolateral and dorsomesial margins with row of slender, sharp spines obscured by setae; ventral surface glabrous. Carpus about 1.3 times as long as merus;

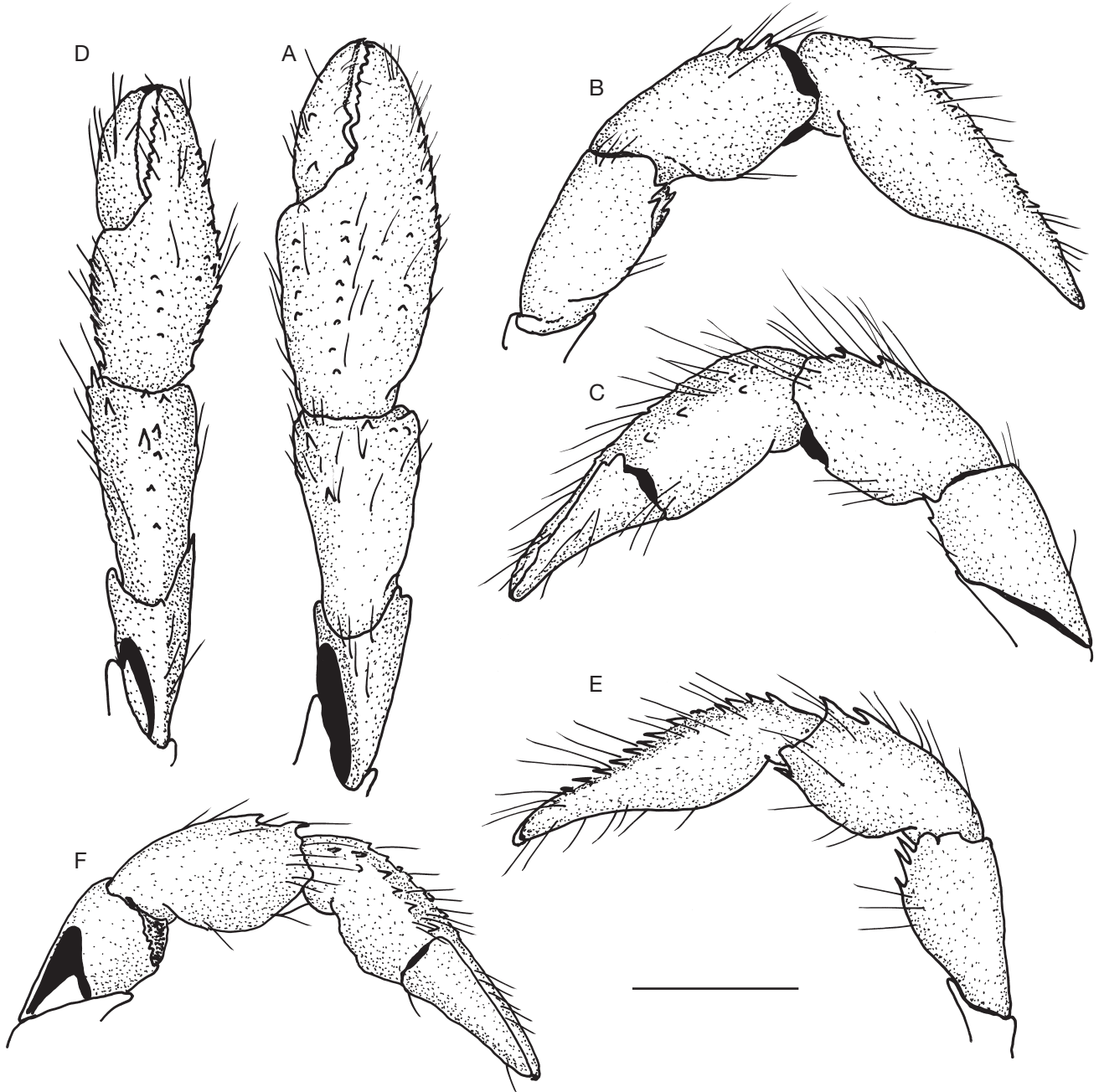


FIG. 14. — *Pagurina bifida* n. gen., n. sp., holotype ♂ 0.8 mm, Guadeloupe, sta GB 34, MNHN-IU-2013-5643: A-C, right cheliped, dorsal view (A), lateral view (B), mesial view (C); D-F, left cheliped, dorsal view (D); lateral view (E); mesial view (F). Scale bar: 0.5 mm.

dorsodistal margin with two small spines, dorsal margin with row of few small spines or tubercles; dorsolateral surface with two sharp spines distally; ventral surface glabrous. Merus unarmed dorsally, nearly naked; ventrolateral and ventromesial margins each with distal row of three or four sharp spines or small tubercles, respectively. Ischium unarmed. Coxa with row of setae on ventromesial distal angle.

#### *Ambulatory legs (Fig. 15A-E)*

With sparse long setae on dorsal margins of segments. Dactyl about 1.4 times as long as propodus, broadly curved, terminating in slender needle-like claw, ventromesial margin with

row of three short corneous spinules. Propodus straight, about 1.5 times as long as carpus, lacking spines. Carpus with two small dorsodistal spines. Merus and ischium lacking spines. Anterior lobe of thoracic sternite XI (between pereopods 3; Fig. 13C) subrectangular, with fringe of short setae on distal margin.

#### *Fourth pereopods (Fig. 15F)*

Semichelate. Dactyl triangular, terminating in strong, sharp corneous claw, lacking preungual process; propodus longer than high, rasp with single row of six rounded corneous scales. Carpus unarmed except for few long setae dorsally. Merus unarmed except for dorsal setae.

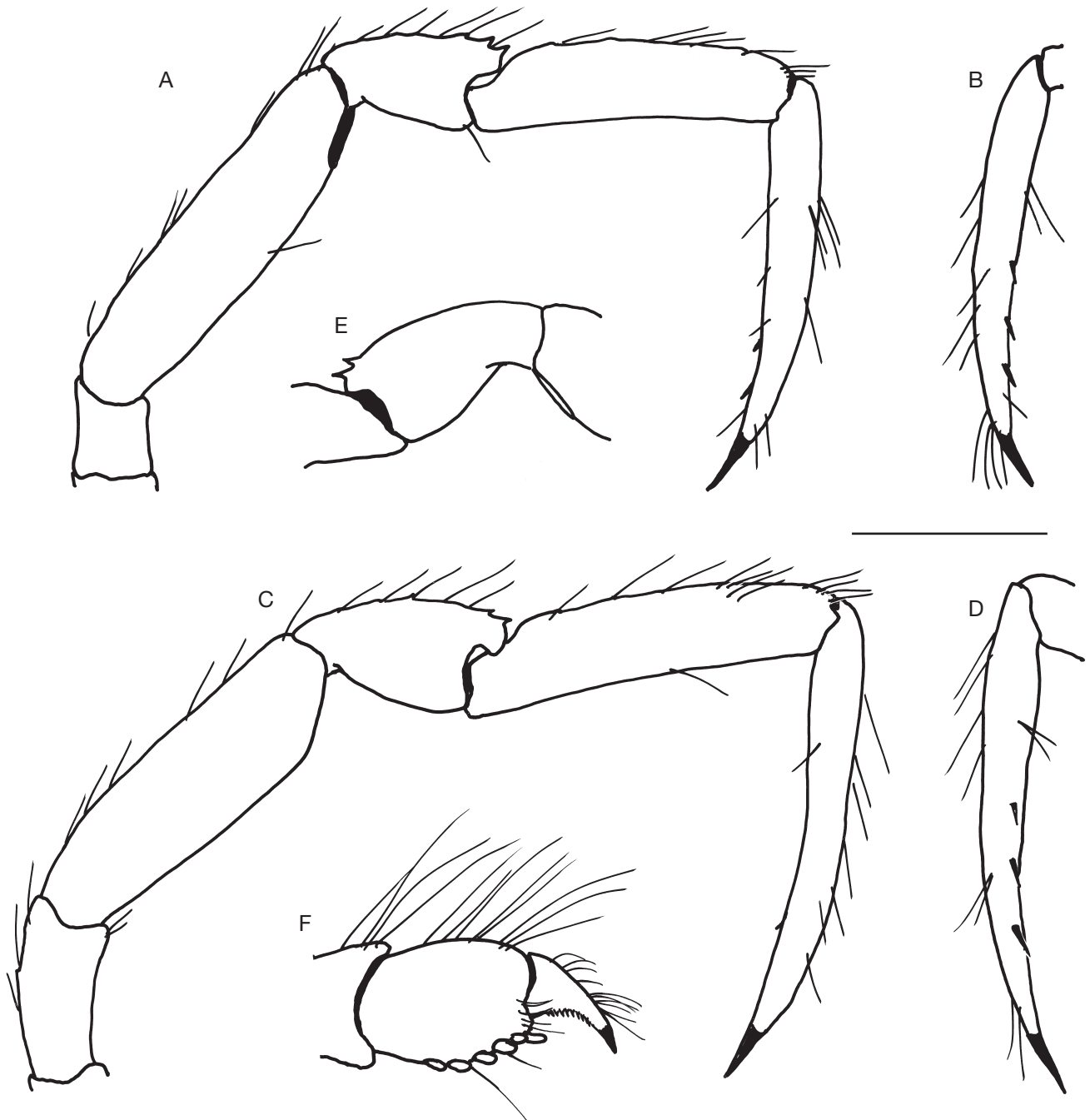


FIG. 15. — *Pagurina bifida* n. gen., n. sp., holotype ♂ 0.8 mm, Guadeloupe, sta GB 34, [MNHN-IU-2013-5643](#): **A**, left pereopod 2, lateral view; **B**, dactyl of same, mesial view; **C**, left pereopod 3, lateral view; **D**, dactyl of same, mesial view; **E**, carpus of same, mesial view; **F**, propodus and dactyl of right pereopod 4, lateral view. Scale bar: 0.5 mm.

#### *Fifth pereopods*

Chelate. Propodal rasp dorsally extending for about half surface of propodus.

#### *Uropods and telson (Fig. 13D)*

Uropods markedly asymmetrical, left largest. Telson nearly symmetrical, longer than broad, with distinct lateral indentations. Anterior and posterior lobes subequal in length. Posterior lobes separated by narrow, median U-shaped cleft; terminal

margins weakly oblique, each armed with row of small spines that includes a distinctly larger and ventrally curved spine on lateral angle, followed on lateral side by smaller spine.

#### *Sexual tubes (Fig. 13C) and pleopods*

Males with paired gonopores; with very short, papilla-like sexual tube protruding from coxa of left gonopore, right coxa lacking sexual tube; with unpaired left pleopods 3-5. Females unknown.

*Genetic data*

See Table 1.

*Colour*

Unknown.

## REMARKS

In addition to the generic characters, *Pagurina bifida* n. gen., n. sp. stands out by the relatively stout ocular peduncles, the relatively strong left cheliped, scant armature on the ventromesial margins of the dactyls of the pereopods 2 and 3 dactyls, and the poorly developed row of scales on the propodal rasp of the pereopod 4. The bifid condition of the ocular acicles is a characteristic of this new species, even though a similar condition occurs in various other species and genera across the Paguridae, including another micro-pagurid described herein as *Pagurellus jenniferae* n. gen., n. sp.

Genus *Paguriscus* n. gen.

TYPE SPECIES. — *Paguriscus robustus* n. gen., n. sp., by present designation. Gender: masculine.

ETYMOLOGY. — The generic name is derived from the genus name *Pagurus*, and using the masculine Greek suffix *-iscus* which denotes something diminutive, in reference to the minute size of specimens in the single species of this new genus.

DIAGNOSIS. — Eight pairs of biserial phyllobranch gills, no pleurobranches on somites X, XI, XII (thoracomeres 5–7, above pereopods 2–4). Rostrum triangular. Ocular acicles simple. Crista dentata with accessory tooth. Chelipeds presumably unequal [left missing in holotype and single specimen known]. Sternite of somite XI (thoracomere 6, pereopod 3) with semi-circular anterior lobe. Pereopod 4 with single row of scales on propodal rasp, dactyl lacking preungual process. Pereopod 5 semi-chelate. Male with coxae of pereopods 5 slightly asymmetrical, trapezoidal in shape, extending posteriorly to form themselves paired sexual tubes; with unpaired, left pleopods 3–5. Telson nearly symmetrical, with weak or obsolete lateral indentations; terminal margins of posterior lobes oblique, with shallow median cleft.

DISTRIBUTION. — Known only from the type species collected in Guadeloupe, Lesser Antilles, Caribbean Sea, at a depth of 19 m.

## REMARKS

Despite the incompleteness of the single male specimen of the new species herein described for this new genus, there is sufficient justification for a new genus based on the unusual low gill number (eight) and formula (lacking pleurobranches), and by the morphology of the coxae and sexual tubes of pereopods 5 in this male. In pagurids, the number of gills is known to vary from 8 to 13 pairs, with the majority having 11. Previous to the discovery of this new genus, only one pagurid species *Decaphyllus barunajaya* McLaughlin, 1997, was known to have eight pairs of gills. However, in *Paguriscus* n. gen., there are two arthrobranches on the third maxilliped, and all pleurobranches have been lost, whereas in *D. barunajaya* there are no arthrobranches on the third maxilliped, and pleurobranches are present on pereopods 3 and 4.

The posteriorly projecting, and slightly asymmetrical coxae of pereopods 5 in the male of *Paguriscus* n. gen. (Fig. 16G), is an unusual condition among genera of Paguridae with sexual tubes. In other pagurids with male sexual tubes, these are present as clearly separate structures from the coxae, whereas in *Paguriscus* n. gen. each coxa consists of a single, calcified tube-like piece. In *Paguriscus* n. gen., the coxae are somewhat similar to the solid, one-piece coxal extensions of males in some coenobitids (see Tudge & Lemaitre 2006), although the similarity can be attributed to evolutionary convergence.

*Paguriscus robustus* n. sp.

(Figs 16, 17; Table 1)

TYPE MATERIAL. — **Holotype.** ♂ 1.3 mm, Guadeloupe, sta GS 20, Port-Louis, outside Grotte aux barracudas, 16°27.34'N, 61°32.07'W, 19 m, 16.V.2012, MNHN-IU-2013-4395.

ETYMOLOGY. — The specific name is from the Latin *robustus*, and refers to the robust coxae of pereopods 5 that in the male of this species form the sexual tubes.

DISTRIBUTION. — Known so far only from Guadeloupe, Lesser Antilles, Caribbean Sea. Depth: 19 m.

HABITAT. — Found living in a gastropod shell.

## DESCRIPTION OF HOLOTYPE

*Shield (Fig. 16A)*

Glabrous, at most with scattered short setae, slightly longer than broad; anterior margin between rostrum and lateral projections weakly concave; anterolateral margins sloping; posterior margin roundly truncate. Rostrum bluntly subtriangular, reaching distally to about same level of lateral projections. Lateral projections subtriangular, terminating in small sharp spine.

*Ocular peduncles*

About 0.6 length of shield; dorsal surface with row of sparse short setae; corneas weakly dilated. Ocular acicles subtriangular, dorsal surface flat; terminating in strong distal spine.

*Antennular peduncles*

Exceeding distal margins of cornea when fully extended by about 0.5–0.7 length of ultimate segment. Ultimate segment naked except for 2 long dorsodistal bristles. Penultimate and basal segments naked; basal segment with blunt ventromesial angle, and small spine on lateral face.

*Antennal peduncles*

Exceeding distal margins of corneas when fully extended by nearly entire length of fifth segment. Fifth and fourth segments unarmed except for scattered short setae. Third segment with strong spine on ventrodistal angle. Second segment with dorsolateral distal angle produced into short simple or bifid spine-like process slightly overreaching

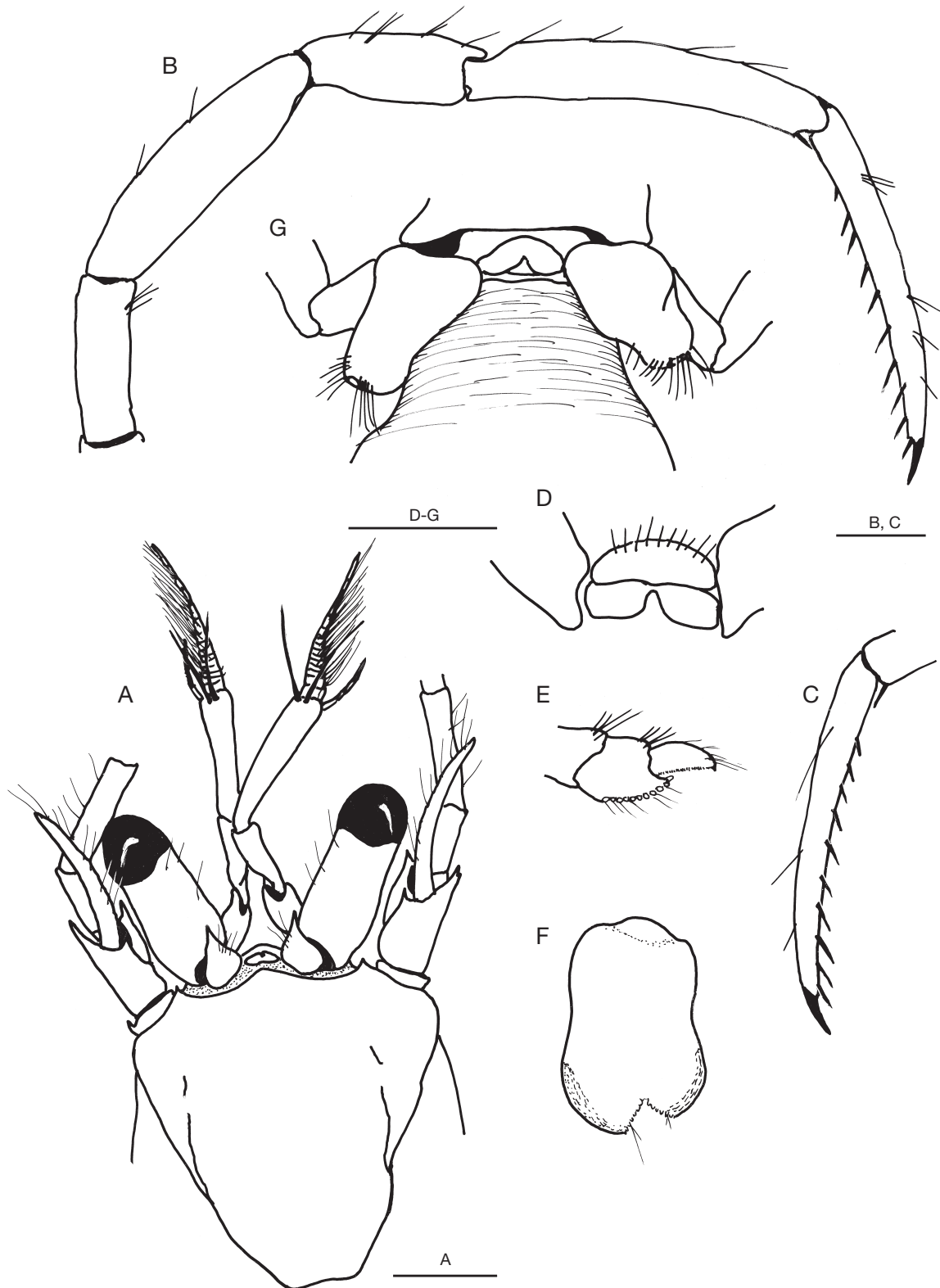


FIG. 16. — *Paguriscus robustus* n. gen., n. sp., holotype ♂ 1.3 mm, Guadeloupe, sta GS 20, [MNHN-IU-2013-4395](#): **A**, shield and cephalic appendages, dorsal view; **B**, right pereopod 3, lateral view; **C**, dactyl of same, mesial view; **D**, sternite XI of third pereopods, ventral view; **E**, propodus and dactyl of right pereopod 4, lateral view; **F**, telson, dorsal view; **G**, coxae of pereopods 5, sternite XIII, and anterior part of pleon, ventral view. Scale bars: 0.5 mm.

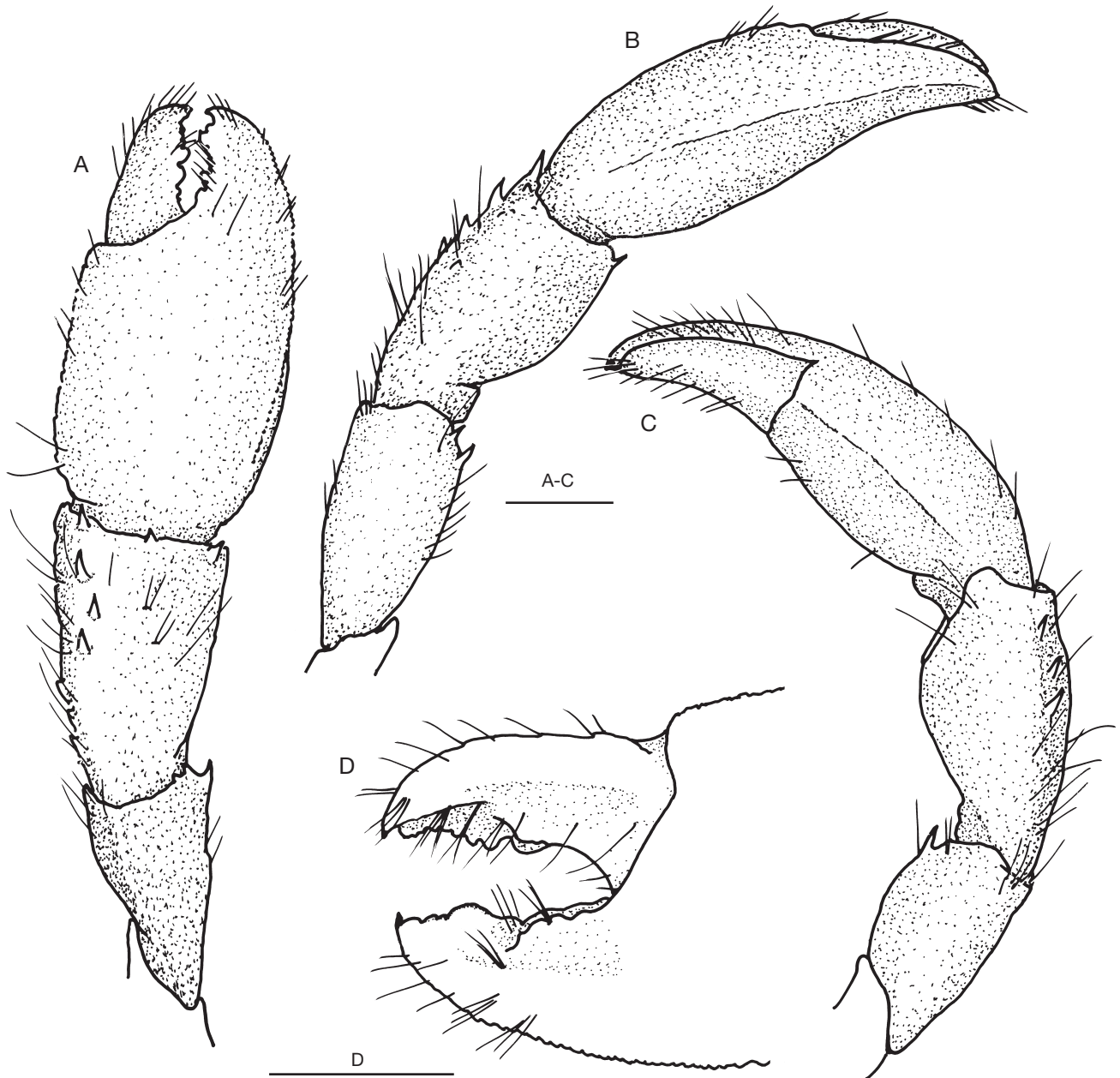


FIG. 17. — *Paguriscus robustus* n. gen., n. sp., holotype ♂ 1.3 mm, Guadeloupe, sta GS 20, MNHN-IU-2013-4395: A–C, right cheliped, dorsal view (A); lateral (B); mesial view (C); D, dactyl and fixed finger of right cheliped, mesial view. Scale bars: 0.5 mm.

distal margin of third segment; dorsomesial distal angle with small spine. First segment with or without minute, curved spine on lateroventral angle. Antennal acicle long, exceeding distal margin of cornea by about 0.3 length of acicle, broadly curving outward and terminating in strong spine, mesial margin with few short setae. Flagella missing in holotype.

#### *Mouthparts*

Mandible, maxillule, and maxilla not dissected. First maxilliped with slender endopod not exceeding distal endite. Second maxilliped without distinguishing char-

acters. Third maxilliped ischium with crista dentata consisting of about 18 subequal, mostly sharp teeth, and one accessory tooth.

#### *Right cheliped* (Fig. 17A–D)

Moderately elongated, mostly glabrous except for scattered short setae. Chela with dorsal and ventral surfaces smooth, lacking spines; fingers each terminating in small, sharp corneous claw slightly overlapping when closed. Dactyl 0.5 length of palm, cutting edge with two large calcareous teeth, and row of fused small teeth forming uneven edge distally; ventromesial face (Fig. 17D) concave

on distal half, somewhat spoon-like distally. Fixed finger similar to dactyl except for cutting edge having larger calcareous teeth more distally, and well defined dorso-lateral margin consisting of faint ridge of minute teeth continued on palm and fading in strength proximally on palm; ventromesial surface concave on proximal half. Palm approximately as long as carpus, dorsally convex; dorsolateral and dorsomesial margins defined by faint and moderately sharp ridge; ventral surface convex, glabrous. Carpus about 1.3 times as long as merus; dorsal surface weakly convex, dorsodistal margin with three small spines (one dorsal, one medial, one lateral), dorsomesial margin with irregular row of sharp spines; lateral face rounded, mesial face flat, nearly vertical; ventral surface convex. Merus subtriangular, distal margin with fringe of short setae; ventrodiscal margins each with one (mesial) and two (lateral) sharp spines. Ischium glabrous. Coxa with row of setae on ventromesial distal angle.

#### *Left cheliped*

Missing in holotype.

#### *Ambulatory legs (Fig. 16B, C)*

Right pereopod 3 (Fig. 16B, C) exceeding right cheliped by about 0.3 length of dactyl, with only scattered short setae or tufts of setae. Dactyl nearly straight, 1.1 times as long as propodus, with ventromesial row of 10 long spinules. Propodus nearly straight, 1.8 times as long as carpus, with long corneous spinule on ventrodiscal angle. Carpus unarmed, dorsodistal angle blunt. Merus and ischium unarmed, somewhat laterally compressed. Anterior lobe of sternite XI (of pereopods 3; Fig. 16D) subsemicircular, with fringe of short setae on distal margin. All other ambulatory legs missing in holotype.

#### *Fourth pereopods (Fig. 16E)*

Semichelate. Dactyl more or less straight, terminating in short, inwardly directed corneous claw, lacking preungual process; propodal rasp with single row of rounded corneous scales. Carpus unarmed except for few short setae dorsally. Merus unarmed except for with dorsodistal tuft of long setae.

#### *Fifth pereopods*

Chelate. Propodal rasp extending on dorsal surface for almost entire length of propodus, and on lateral surface for about one-third length of propodus.

#### *Uropods and telson (Fig. 16F)*

Uropods markedly asymmetrical, left largest. Telson nearly symmetrical, longer than broad, with weak lateral indentations. Anterior lobes longer than posterior lobes. Posterior lobes nearly symmetrical, outline of margins together forming semi-circle, with chitinous lateral margins, separated by narrow, shallow median cleft; terminal margins oblique, armed with row of minute blunt spines and few short setae.

#### *Sexual tubes (Fig. 16G) and pleopods*

Males with coxae of pereopods 5 extended posteriorly as paired, subequal, stout and calcified sexual tubes trapezoid in shape, tube openings each with lip-like edge fringed by setae; with unpaired left pleopods 3-5. Females unknown.

#### *Genetic data*

See Table 1.

#### *Colour*

Unknown.

#### REMARKS

The single male specimen of this new species was collected as part of the epifauna on rocky bottom. The specimen is missing pereopods 1-3 except for the right cheliped and right pereopod 3. It is distinctive in the following characters: 1) coxae of pereopods 5 in the male extended posteriorly forming a pair of symmetrical trapezoidal sexual tubes; 2) right chela smooth, glabrous, lacking spines or setae, the mesial margin of the palm, and the dorsolateral margins of the fixed finger and anterior half of palm each weakly but distinctly delimited by a low, minutely denticulate ridge; 3) posterior lobes of telson have rounded lateral margins, the outlines of which together form a semi-circle, and the terminal margins are oblique and minutely armed; 4) ultimate antennular segment with pair of long dorsodistal bristles; and 5) antennal acicles long, exceeding corneas by one-third length of acicle. Other diagnostic characters include the rounded rostrum, ocular acicles terminating in single spine, and the propodal rasp of pereopod 4 with only one row of ovate scales.

#### Genus *Paguruncio* n. gen.

TYPE SPECIES. — *Paguruncio parvulus* n. gen., n. sp., by present designation. Gender: masculine.

ETYMOLOGY. — The generic name is derived from the genus name *Pagurus*, and using the masculine Latin suffix *-uncio* which denotes something diminutive, in reference to the minute size of specimens in the single species of this new genus.

DIAGNOSIS. — Eight pairs of biserial phyllobranch gills, no gill on third maxilliped and cheliped, no pleurobranches on somites X, XI (thoracomeres 5, 6, above pereopods 2 and 3). Rostrum broadly triangular. Ocular acicles terminating in simple spine. Ischium with accessory tooth. Chelipeds subequal in length, right not much stronger than left. Sternite of somite XI (thoracomere 6, pereopod 3) with subrectangular anterior lobe. Pereopod 4 with single row of scales on propodal rasp, dactyl lacking preungual process. Pereopod 5 semi-chelate. Male with paired, subequal, slender, membranous sexual tubes directed posteriorly, on coxae of pereopods 5; pleopod condition unknown. Female with paired gonopores; pleopod condition incompletely known except for presence of unpaired left pleopod 5. Telson nearly symmetrical, with lateral indentations; terminal margins oblique, armed with spines.

DISTRIBUTION. — Known based on the type species found in Curaçao, at a depth of 224 m

## REMARKS

There is no clear morphological relationship or similarity between the single species of *Paguruncio* n. gen. and the other species described in this report that also have male sexual tubes. *Paguruncio*, n. gen. and *Paguriscus* n. gen. both have paired, subequal sexual tubes, although the tubes are morphologically different (Figs 16G; 18E). Both new genera have eight pairs of biserial gills; however, the gill formula is quite different in the two (see respective Diagnoses).

*Paguruncio parvulus* n. sp.  
(Figs 18-20; Table 1)

TYPE MATERIAL. — **Holotype.** ♀ 0.4 mm, Curaçao, ARMS 17, 224 m, BCURA 0952, USNM 1297508.

**Paratypes.** Curaçao: 1 ♂ 0.6 mm (missing left chelipeds, ambulatory legs and pleon), ARMS 23, 91.4 m, BCURA 1557, USNM 1297613.

ETYMOLOGY. — The specific name is from the Latin *parvulus*, meaning small, tiny, and refers to the very small size of individuals of this new species.

DISTRIBUTION. — So far known only from Curaçao, where it was collected on ARMS. Depth: 91.4-224 m.

## DESCRIPTION

*Shield (Fig. 18A)*

Weakly subtriangular or nearly ovate, glabrous except for few setae near rostrum, about 1.2 times as long as broad; anterior margin between rostrum and lateral projections weakly concave; anterolateral margins sloping; posterior margin roundly truncate. Rostrum bluntly and broadly subtriangular, reaching slightly beyond level of lateral projections. Lateral projections subtriangular, each terminating in sharp spine.

*Ocular peduncles*

About 0.7 length of shield, glabrous; corneas weakly dilated. Ocular acicles subtriangular, dorsal surface flat; terminating in strong spine.

*Antennular peduncles*

Exceeding distal margins of cornea when fully extended by about 0.5 length of ultimate segment. Ultimate, penultimate and basal segments naked; basal segment with blunt ventromesial angle, and small spine on lateral face.

Antennal peduncles exceeding distal margins of corneas when fully extended by about 0.5 length of fifth segment. Fifth and fourth segments unarmed except for scattered short setae. Third segment with small spine on ventrodiscal angle. Second segment with dorsolateral distal angle produced into spine-like process reaching to about distal margin of third segment; dorsomesial distal angle with small spine. First segment unarmed. Antennal acicle not exceeding distal margin of cornea, broadly curving outward and terminating in strong spine, mesial margin with few distal setae. Flagella long, slightly exceeding tip of right cheliped, with few short setae < 1 flagellar article in length.

*Mouthparts*

Not dissected. Third maxilliped ischium with crista dentata consisting of row of about 12 small teeth, and one accessory tooth.

*Right cheliped (Fig. 19A, B)*

Chelipeds nearly equal in length, right largest but not massive. Right cheliped with scattered setae. Chela ovate, with dorsal and ventral surfaces smooth, lacking armature. Fingers each terminating in sharp corneous claw slightly overlapping when closed. Dactyl subequal in length to palm, cutting edge with two large calcareous teeth on proximal half, and row of fused small teeth distally; mesial margin rounded or weakly defined; ventral face convex, smooth. Fixed finger similar to dactyl except for cutting edge having one large calcareous tooth; dorsolateral margin defined by weak ridge of minute tubercles continued posteriorly for about 0.7 of palm; ventromesial face convex, smooth. Palm about as long as broad, dorsal surface convex, unarmed except for scattered short setae, and dorsolateral ridge extending from fixed finger; mesial face rounded; ventral surface convex. Carpus about 1.8 times as long as broad, subequal to merus in length; dorsal surface weakly convex or somewhat flattened, unarmed except for row of dorsomesial small blunt or sharp spines; lateral face rounded, mesial face flat, nearly vertical; ventral surface glabrous. Merus subtriangular in cross-section; ventral face smooth, ventrolateral and ventromesial margins with distal row of sharp spines. Ischium glabrous. Coxa with row of setae on ventromesial distal angle.

*Left cheliped (Fig. 19C, D)*

Elongate, glabrous or at most with scattered short setae; dactyl and fixed finger each terminating in sharp corneous claw, slightly overlapping when closed, cutting edge of dactyl consisting of row of mostly fused minute corneous teeth, cutting edge of fixed finger with minute calcareous teeth interspersed with fused corneous teeth. Dactyl about 1.2 times as long as palm; dorsal, mesial, and ventral surfaces rounded. Palm dorsal surface with weakly raised longitudinal median row of small tubercles or spines; ventral surface convex, smooth. Carpus about as long as merus; dorsal surface somewhat flat, with a few long bristles, dorsodistal margin with two or three small spines; dorsolateral and dorsomesial margins each with row of two or three small spines; ventral surface convex. Merus subtriangular in cross-section; ventrolateral and ventromesial margins each with row of small sharp spines. Ischium glabrous. Coxa with row of setae on ventromesial distal angle.

*Ambulatory legs (Fig. 20A-D)*

Exceeding tip of chelipeds by about 0.2 length of dactyls when fully extended, sparsely setose. Dactyl broadly curved, about 1.2 times as long as propodus, terminating in sharp corneous claw; with ventromesial row of four or five slender corneous spinules arranged in acute angle to dactyl margin. Propodus nearly straight; with few setae on dorsal and ventral margins, lateral and mesial faces glabrous. Carpus with blunt dorsodistal angle, and few setae on dorsal margin. Merus somewhat

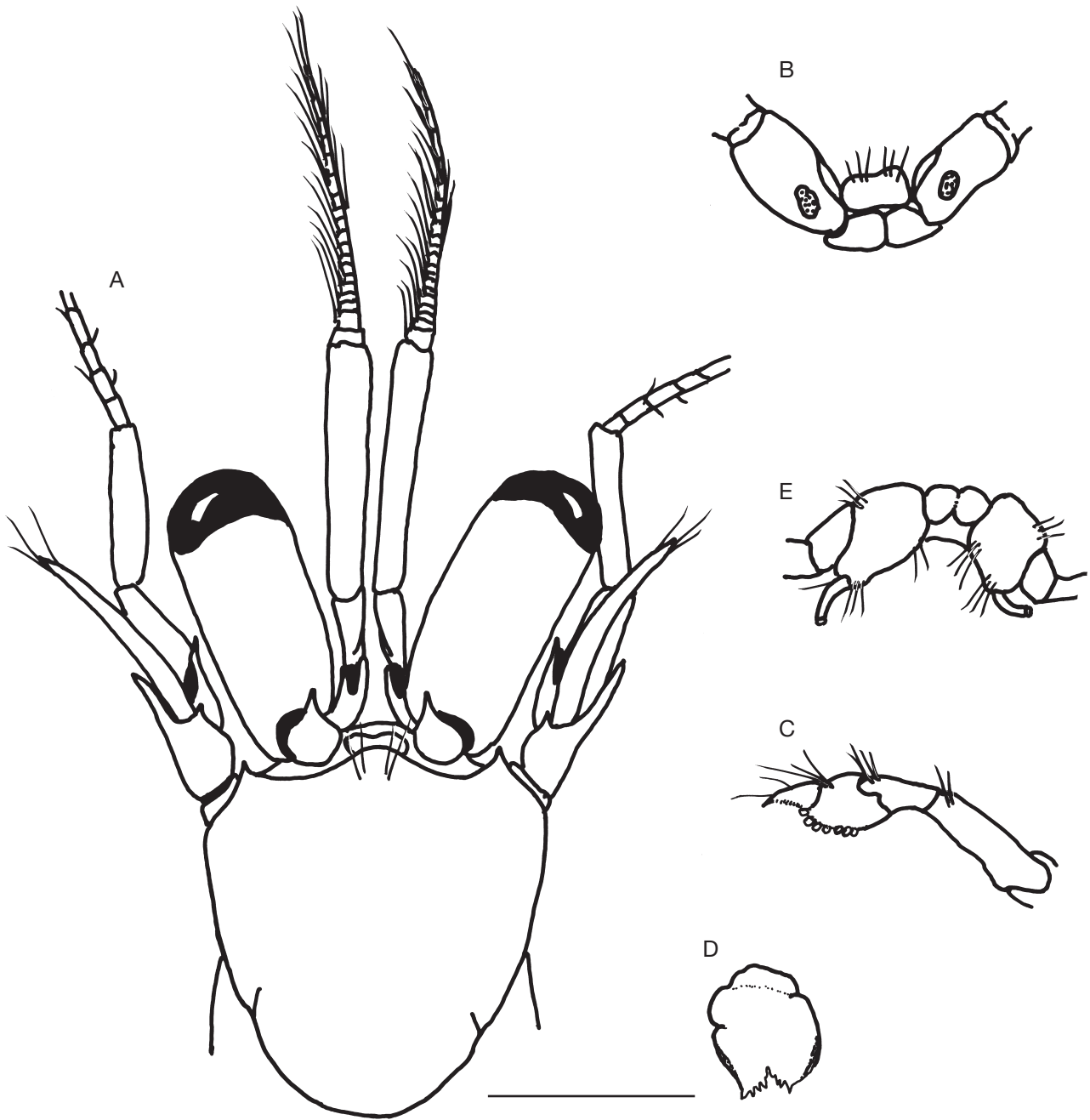


FIG. 18. — *Paguruncio parvulus* n. gen., n. sp.: **A–D**, holotype ♀ 0.4 mm, Curaçao, ARMS 17, USNM 1297508; **E**, paratype ♂ 0.6 mm, ARMS 23, USNM 1297613. **A**, shield and cephalic appendages, dorsal view; **B**, sternite XI and coxae of third pereopods, ventral view; **C**, propodus and dactyl of right pereopod 4, lateral view; **D**, telson, dorsal view. Scale bar: 0.5 mm.

laterally compressed, lateral and mesial faces glabrous, dorsal margin with few setae; ventral margin with row of several long, well spaced setae. Ischium unarmed. Anterior lobe of sternite XI (of pereopods 3; Fig. 18B) subrectangular, with fringe of setae on distal margin.

#### *Fourth pereopod 4 (Fig. 18C)*

Semichelate. Dactyl weakly curved, terminating in short, inwardly directed corneous claw, lacking preungual process; propodal rasp with single row of ovate corneous scales. Carpus

unarmed except for few short setae dorsally. Merus unarmed except for with dorsodistal tuft of long setae.

#### *Fifth pereopods*

Chelate. Propodal rasp extending on dorsal surface for about 0.7 length of propodus.

#### *Uropods and telson (Fig. 18D)*

Uropods markedly asymmetrical, left largest. Telson nearly symmetrical, slightly longer than broad, with distinct lateral

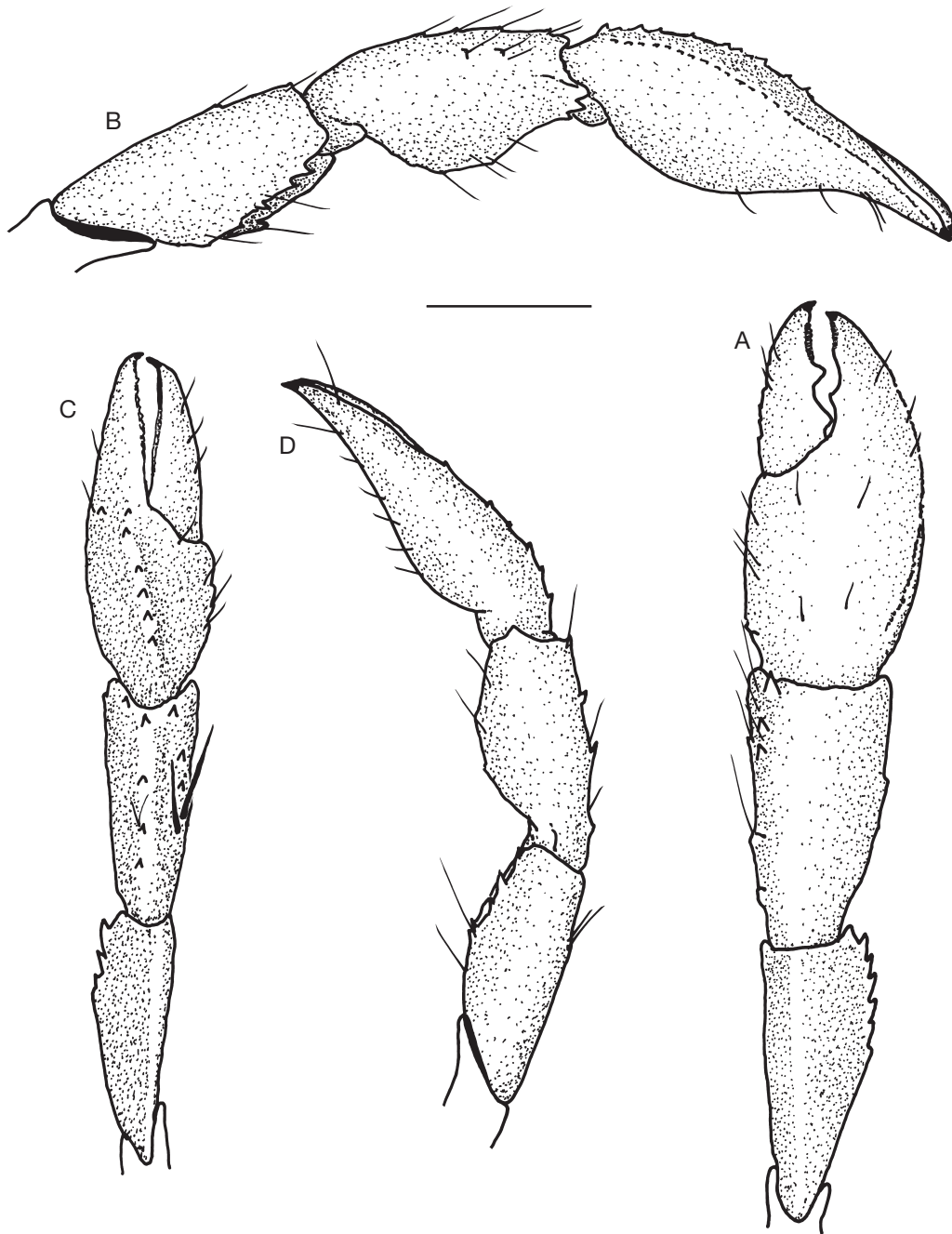


FIG. 19. — *Paguruncio parvulus* n. gen., n. sp., holotype ♀ 0.4 mm, Curaçao, ARMS 17, USNM 1297508: **A**, right cheliped, dorsal view; **B**, same, lateral view; **C**, left cheliped, dorsal view; **D**, same lateral view. Scale bar: 0.5 mm.

indentations; anterior shorter than posterior lobes; posterior lobes with chitinous lateral margins, lobes separated by narrow U-shaped median cleft, terminal margins oblique, each armed with four or five spines, lateral most strongest and somewhat curved ventrolaterally.

#### *Sexual tubes (Fig. 18E) and pleopods*

Males with coxae of pereopods 5 somewhat asymmetrical, right largest, slightly extending posteriorly and each with

very short, membranous slender sexual tube directed posteriorly and curving dorsally; pleopod condition unknown (single known male paratype missing pleon). Females with paired gonopores; pleopod condition undetermined except for presence of left pleopod 5 (single known female holotype missing other pleopods).

#### *Genetic data*

See Table 1.

## Colour

Unknown

## REMARKS

As previously mentioned under the genus *Paguruncio*, *Paguruncio parvulus* n. gen., n. sp. and *Paguriscus robustus* n. gen., n. sp. have paired subequal sexual tubes and the same total number of gills, but the morphology of the tubes and branchial formulas are markedly different. The sexual tubes in *Paguruncio parvulus* n. gen., n. sp. consist of slightly expanded coxae each with a short, slender, membranous extension (Fig. 18E), whereas in *Paguriscus robustus* n. gen., n. sp. the coxae are considerably expanded and lack any membranous extensions. In other features, these two species also differ markedly, most notably in the shape and armature of the dactyls of pereopods 2 and 3, as well as the telson shape and armature (compare Figs 16C, F with Figs 18D; 20B, D). The gill formula in *Paguruncio parvulus* n. gen., n. sp. is 0 gill on third maxilliped, one arthrobranch on the cheliped, two arthrobranches on pereopod 2, two arthrobranches on pereopod 3, and three gills (one pleurobranch, two arthrobranches) on pereopod 4; whereas in *Paguriscus robustus* n. gen., n. sp. there are two arthrobranches on third maxilliped, cheliped and pereopod 2, and one arthrobranch on each of pereopods 3 and 4.

## Genus *Pagurus* Fabricius, 1775

*Pagurus* Fabricius, 1775: 410 (in part). — McLaughlin 1974: 37; 1997: 525; 2003: 125. — McLaughlin *et al.* 2010: 32.

TYPE SPECIES. — *Cancer bernhardus* Linnaeus, 1758, by subsequent designation by Latreille (1810: 422).

## REMARKS

For a complete taxonomic history and diagnosis of *Pagurus*, see McLaughlin (1974).

### *Pagurus abditus* n. sp. (Figs 21–24; Table 1)

TYPE MATERIAL. — **Holotype.** ♀ 0.8 mm, Curaçao, ARMS 16, 91 m, 15.IX.2015, BCURA 0924, USNM 1297485.

**Paratypes.** Curaçao: 1 ♂ 0.8 mm, ARMS 13, 115.8 m, 15.IX.2015, BCURA 0605, USNM 1297441 (ULLZ 16885); 1 ♀ 0.7 mm, ARMS 16, 91 m, 15.IX.2015, BCURA 0780, USNM 1297489; 1 ovig ♀ 0.9 mm, ARMS 31, 91.4 m, 16.X.2016, BCURA 2555, USNM 1292078; 1 ovig ♀ 0.8 mm, ARMS 33, 225.5 m, 16.X.2016, BCURA 2754, USNM 1292079.

ETYMOLOGY. — The specific name is derived from the Latin *abditus*, meaning hidden, concealed, and refers to the cryptic nature of this new species that contributed to hide its discovery until now.

DISTRIBUTION. — Known so far only from deep reefs in Curaçao, where it has been found living in ARMS. Depth: 91–115.8 m.

HABITAT. — Found living in gastropod shells, only in ARMS.

## DESCRIPTION

### *Gills and shield* (Fig. 21A)

Eight pairs of biserial phyllobranch gills (no pleurobranch on thoracomere above pereopod 4). Shield glabrous, about as long as broad; anterior margin between rostrum and lateral projections weakly concave; anterolateral margins sloping; posterior margin roundly truncate. Rostrum broadly triangular or nearly obsolete, reaching distally to about same level of lateral projections. Lateral projections subtriangular, terminating in small sharp spine.

### *Ocular peduncles*

Relatively long, about 0.8 length of shield; dorsal surfaces naked or with scattered short setae; corneas weakly dilated. Ocular acicles subtriangular, terminating in strong, simple spine.

### *Antennular peduncles*

At most slightly exceeding distal margins of cornea when fully extended. Segments naked or with scattered short setae; basal segment with blunt ventromesial distal angle, and small spine on lateral face.

### *Antennal peduncles*

Not exceeding distal margins of corneas when fully extended, reaching to about proximal margins of cornea. Fifth and fourth segments unarmed except for scattered short setae. Third segment with spine on ventrodistal angle. Second segment with dorsolateral distal angle produced into spine-like process; dorsomesial distal angle with small spine. First segment with small lateral spine. Antennal acicles not reaching proximal margins of corneas, broadly curving outward, terminating in strong spine, mesial margin with few setae distally. Flagellum short, not exceeding extended right cheliped, with setae 1 to 2 flagellar articles in length.

### *Mouthparts*

Not dissected. Third maxilliped ischium with crista dentata consisting of about 15 small, subequal teeth, and strong accessory tooth.

### *Right cheliped* (Fig. 22A, B)

Chelipeds unequal in strength, short and stout, right distinctly stronger than left, with sparse setae. Right cheliped (Fig. 22A, B) with chela about 1.3 times as long as broad, dactyl and fixed finger each terminating in small, inwardly curved corneous claw slightly overlapping when closed; chela ventral surface glabrous. Dactyl about as long as palm, dorsally with short median row of spines, mesial margin with row of small spines; cutting edge with two or three unequal, rounded calcareous teeth, and row of fused small teeth distally. Fixed finger with short irregular row of small blunt spines dorsally; dorsolateral margin well defined by row of small spines continued for half or more of palm; cutting edge with one large rounded calcareous tooth medially, and row of small corneous teeth distally. Palm approximately as long as carpus, dorsally convex; dorsal surface with irregular

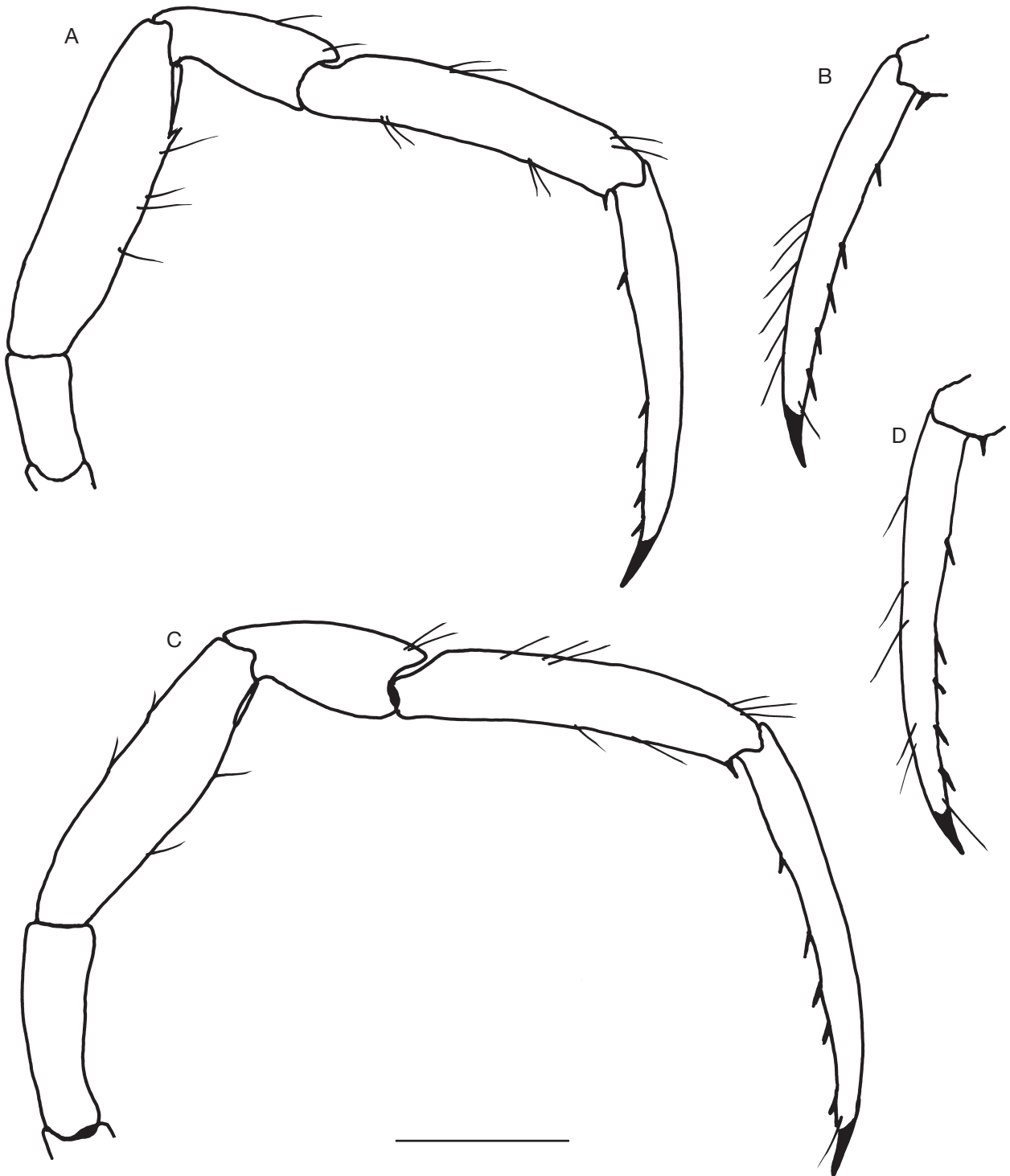


FIG. 20. — *Paguruncio parvulus* n. gen., n. sp., holotype ♀ 0.4 mm, Curaçao, ARMS 17, USNM 1297508: **A**, right pereopod 2, lateral view; **B**, dactyl of same, mesial view; **C**, right pereopod 3, lateral view; **D**, dactyl of same, mesial view. Scale bar: 0.5 mm.

short, longitudinal rows of small spines; dorsolateral margin well defined by row of small spines; dorsomesial margin with row of small spines; ventral surface convex, shiny and lacking spines. Carpus dorsal surface weakly convex; dorsodistal margin unarmed; dorsomesial margin with row of five spines; lateral and mesial faces nearly flat, ver-

tical; ventral surface weakly convex. Merus subtriangular in cross-section, dorsodistal margin unarmed except for short setae; ventrolateral margin with row of small spines distally, ventromesial margin unarmed or with one or two small spines. Ischium unarmed. Coxa with row of setae on ventromesial distal angle.

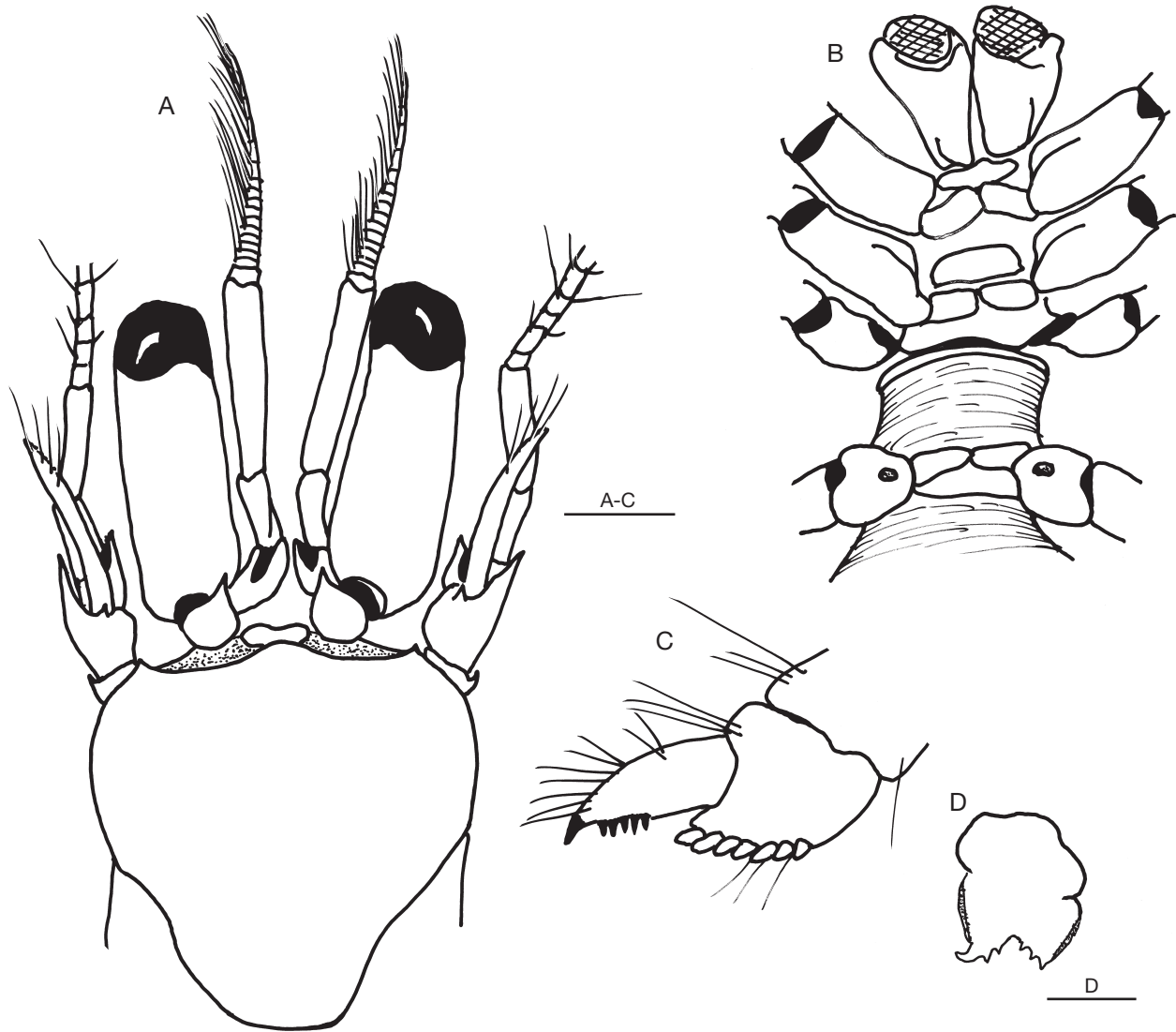


FIG. 21. — *Pagurus abditus* n. sp., Curaçao: **A, C, D**, holotype ♀ 0.8 mm, ARMS 16, USNM 1297485; **B**, paratypes ♂ 0.8 mm, ARMS 13, USNM 1297441; **A**, shield and cephalic appendages, dorsal view; **B**, sternites IX-XIII, and coxae of chelipeds and pereopods 2-5, ventral view; **C**, propodus and dactyl of right pereopod 4, lateral view; **D**, telson, dorsal view. Scale bars: A-C, 0.25 mm; D, 0.1 mm.

#### *Left cheliped (Fig. 22C, D)*

Relatively strong; carpus and chela about half as wide as same segments of right cheliped, sparsely setose, ventral surfaces glabrous; dactyl and fixed finger each terminating in sharp corneous claw slightly overlapping when closed, cutting edges consisting of fused row of minute teeth. Dactyl about 0.5 as long as palm; dorsal and ventral surfaces rounded, unarmed. Palm dorsal surface with distinctly raised longitudinal median ridge armed with double row of small spines continued on fixed finger; mesial face sloping, unarmed or with few small tubercles; ventral surface unarmed. Carpus slightly longer than merus; dorsodistal margin with two or three small spines medially; with dorsolateral and dorsomesial row of small spines; lateral and mesial faces sloping; ventrolateral margins with small blunt

spines distally; ventral surface unarmed. Merus subtriangular in cross-section, unarmed except for row of setae on dorsal margin; ventrolateral margin with row of sharp spines distally. Ischium unarmed. Coxa with row of setae on ventromesial distal angle.

#### *Ambulatory legs (Fig. 23A-E)*

Sparsely setose, subequal left from right, except for right pereopod 3 with slightly shorter and higher propodus and dactyl, and different spination on ventral margins of dactyl and propodus. Right pereopod 3 with dactyl about 5.3 times longer than high (vs 6.4 in other ambulatory legs), propodus about 2.8 longer than high (vs 4.1 in other ambulatory legs); ventral margin of dactyl and ventrodistal margin of propodus with row of microscopic, short corneous spinules

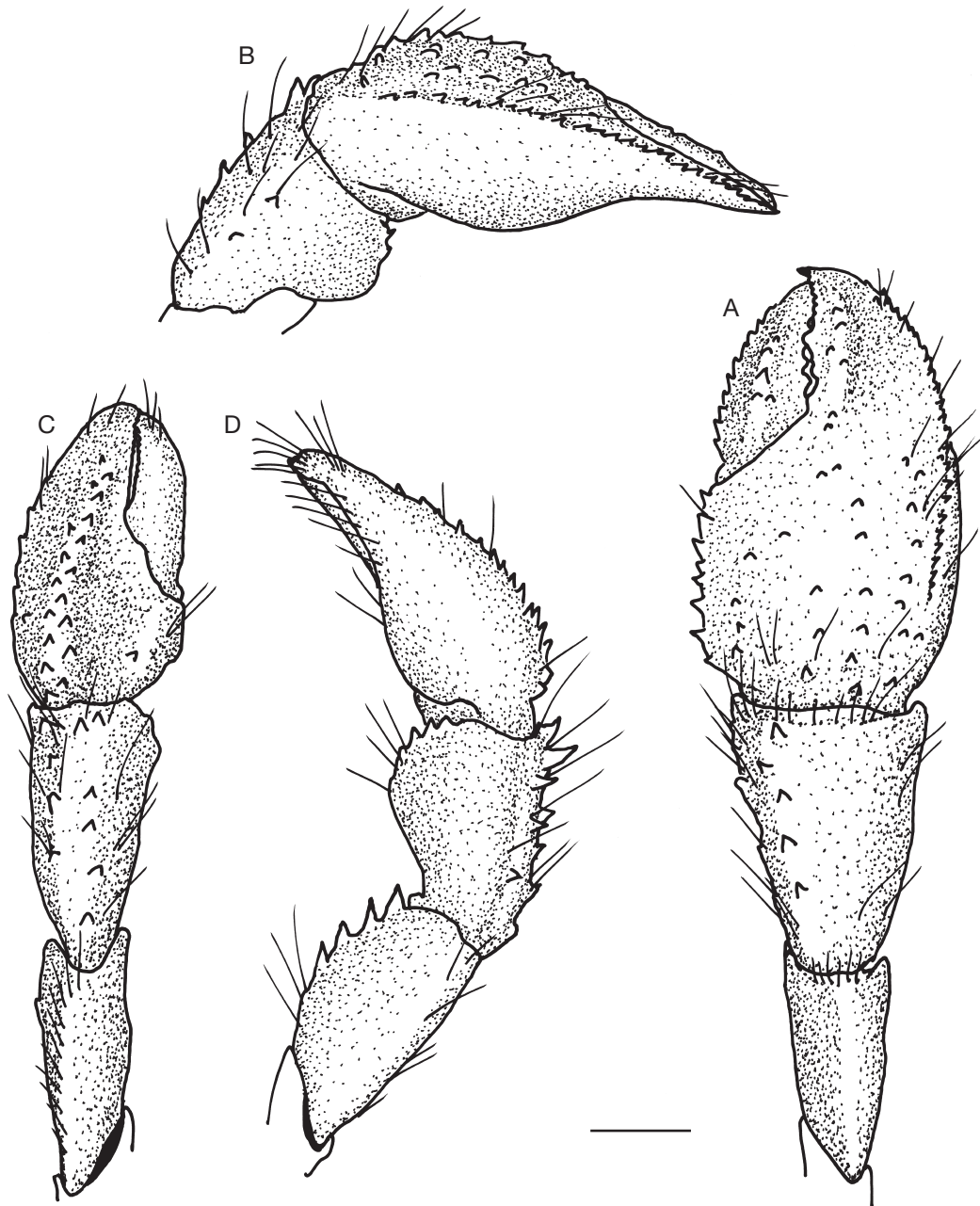


FIG. 22. — *Pagurus abditus* n. sp., holotype ♀ 0.8 mm, Curaçao, ARMS 16, USNM 1297485: **A**, **B**, right cheliped, dorsal view (**A**), carpus and chela of same, lateral (**B**); **C**, **D**, left cheliped, dorsal (**C**); lateral (**D**). Scale bar: 0.25 mm.

in addition to six long, slender corneous spinules (Fig. 23B). Dactyls of other ambulatory legs about 1.1 times as long as propodus, broadly curved, terminating in sharp corneous claw, ventromesial margin with row of usually six corneous spinules. Propodus nearly straight or broadly curved, about 1.2 times as long as carpus, lacking spines except for slender corneous spinule on ventrodiscal angle. Carpus with small dorsodistal spine. Merus unarmed or with 1–3 small spines on ventrodiscal margin. Ischium unarmed. Anterior lobe of sternite XI (of pereopods 3; Fig. 21B) subrectangular, naked distally.

#### *Fourth pereopods (Fig. 21C)*

Semichelate. Dactyl nearly straight, slender, terminating in short, inwardly directed corneous claw, lacking preungual process, with distal row of small blunt teeth; propodal rasp with single row of ovate corneous scales. Carpus unarmed except for few short setae dorsally. Merus unarmed except for with dorsodistal tuft of long setae.

#### *Fifth pereopods*

Chelate. Propodal rasp dorsally extending for about 0.3 length of propodal surface.

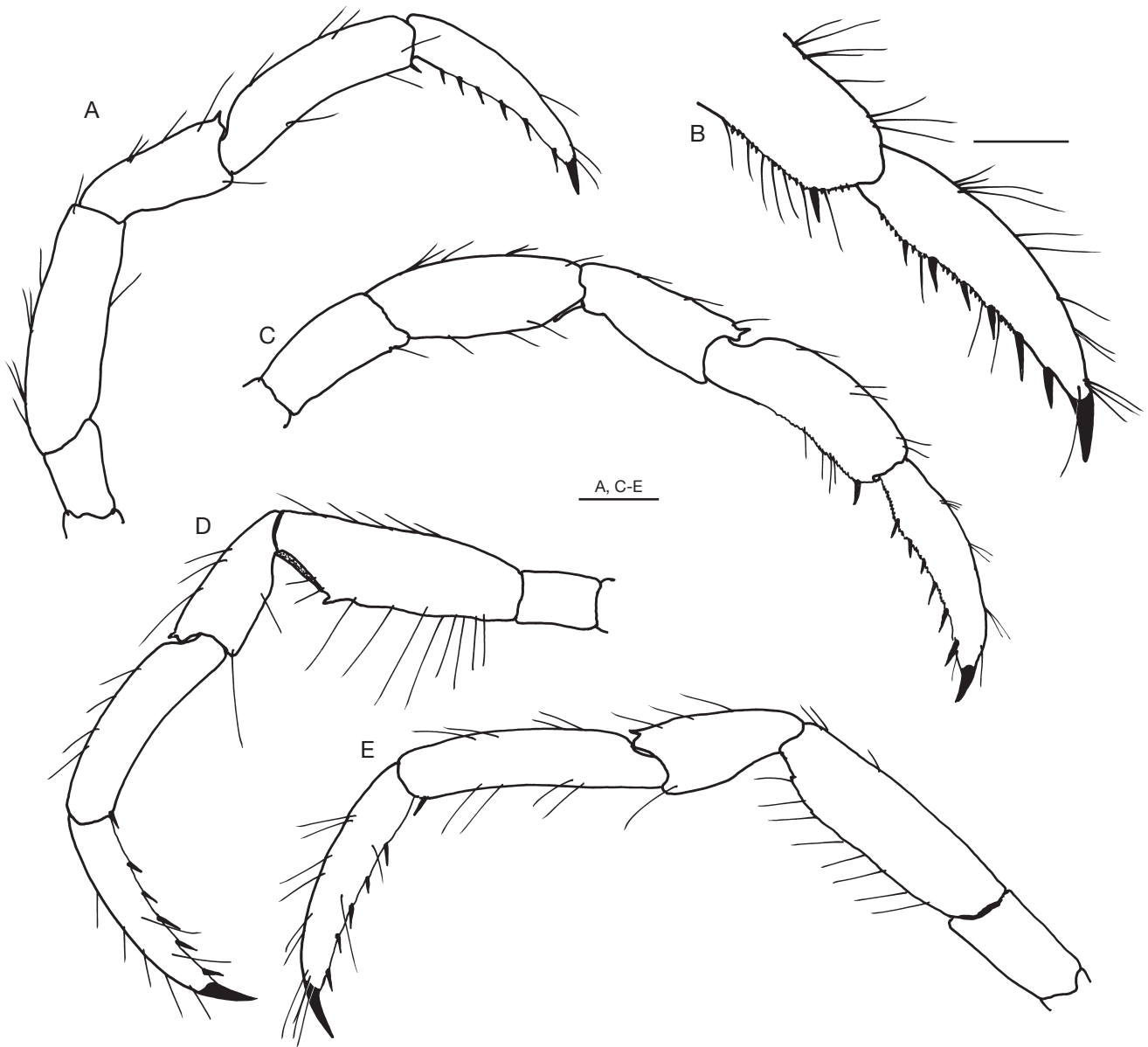


FIG. 23. — *Pagurus abditus* n. sp., holotype ♀ 0.8 mm, Curaçao, ARMS 16, USNM 1297485: **A**, right pereopod 2, lateral; **B**, dactyl of right pereopod 3, lateral view; **C**, right pereopod 3, lateral view; **D**, left pereopod 2, lateral view; **E**, left pereopod 3, lateral view. Scale bar: A, C-E, 0.25 mm; B, 0.1 mm.

#### *Uropods and telson (Fig. 21D)*

Uropods markedly asymmetrical, left largest, exopods each with row of long setae dorso- and ventrodistally. Telson weakly symmetrical, about as long as broad, with distinct lateral indentations; posterior lobes separated by U-shaped median cleft, terminal margins weakly oblique, each armed with row of 2 small spines in addition to laterodistal spine, latter distinctly stronger and outwardly curved on left lobe.

#### *Gonopores and pleopods (Fig. 21B)*

Males with paired gonopores and no sexual tubes; with unpaired left pleopods 3-5. Females with unpaired left pleopods 2-5 (ovigerous females unknown).

#### *Genetic data*

See Table 1.

#### *Colour (Fig. 24)*

Shield mottled with whitish and orange patches. Ocular peduncles transparent to pale blue translucent with light orange stripes; corneas white. Antennules and antennal peduncles lavender to translucent blue. Chelipeds mostly orange except for whitish distal portions of fingers, dorsomesial margin of right palm, spines on meri, carpi and chelae, and distal portion meri. Ambulatory legs colored on meri and propodi with broad band of light maroon to rust orange proximally and broad band of white distally.



FIG. 24. — *Pagurus abditus* n. sp., Curaçao: **A**, paratype ♂ 0.8 mm (dismembered), ARMS 13, USNM 1297441 (ULLZ 16885), dorsal view; **B**, paratype ovig ♀ 0.9 mm, ARMS 31, USNM 1292078.

#### REMARKS

*Pagurus abditus* n. sp. falls under the current broad definition of *Pagurus* Fabricius, 1775, although it does not fit in any of the 11 informal groups defined to accommodate many, but not all, of the species currently assigned to this genus (e.g., McLaughlin 1974; Nucci & Melo 2003; Lemaitre & Cruz Castaño 2004; Olguín & Mantelatto 2013; Komai & Rahayu 2014). In particular, the peculiar morphology of the propodus and dactyl (Fig. 23B) of the right pereopod 3 in this new species is unique among western Atlantic congeners, and suggests that *P. abditus* n. sp. might represent a different clade from those presumably represented by the 11 informal groups of *Pagurus*. Curiously, *P. abditus* n. sp. is the second species of *Pagurus* recently discovered in the southern Caribbean that exhibits a unique, albeit different, morphology of the propodus and dactyl of pereopod 3. The other species, *P. scopaeopsis* Lima & Lemaitre, 2016, can be distinguished from all other tropical western Atlantic congeners by the presence of dense brush-like setation on the ventromesial margin of the dactyl of left pereopod 3.

#### Genus *Pusillopagurus* n. gen.

TYPE SPECIES. — *Pusillopagurus polulus* n. gen., n. sp., by present designation. Gender: masculine.

ETYMOLOGY. — The generic name is a combination of the genus name *Pagurus* with the Latin *pusillus*, which refers to something very small, and used in reference to the minuscule size of specimens in the single species of this new genus.

DISTRIBUTION. — Known based on the type species found in Curaçao, at a depth of 15.2–115.8 m.

DIAGNOSIS. — Eight pairs of biserial phyllobranch gills, only 1 pleurobranch on somite XII (thoracomere 7, above pereopod 4). Rostrum triangular. Ischium edge of crista dentata projected medially, lacking accessory tooth. Chelipeds subequal in length, somewhat slender. Sternite of somite XI (thoracomere 6, pereopod 3) with anterior

lobe subrectangular, bilobed. Pereopod 4 with single row of scales on propodal rasp, dactyl lacking preungual process. Pereopod 5 semi-chelate. Male with coxae of pereopods 5 symmetrical, with paired, unequal sexual tubes, right tube much longer than left, distally coiled and filamentous, left tube not coiled or filamentous; with unpaired, left pleopods 3–5. Female with paired gonopores, and unpaired, left pleopods 2–5. Telson nearly symmetrical, longer than broad, with lateral indentations dividing anterior and posterior lobes; terminal margins of posterior lobes weakly oblique, armed with distinct spines.

#### REMARKS

There are no clear morphological similarities between this new genus and other known pagurid genera in which the male has sexual tubes, despite some having similar sexual tubes. As in *Pusillopagurus* n. gen. and at least 18 other pagurid genera in which the male has paired sexual tubes, the right is longer than the left. In general morphology, the tubes of *Pusillopagurus* n. gen. are most similar to those of *Trichopagurus* de Saint Laurent (1970b)], and to a lesser extent those of *Alainopaguroides* McLaughlin, 1997 and *Icelopagurus* McLaughlin, 1997. However, in most other important morphological features, such as the cephalic shield and appendages, third maxilliped crista dentata, chelipeds, ambulatory legs, and telson, *Pusillopagurus* n. gen. differs markedly from these three genera. Furthermore, the number of gills in this new genus is eight, whereas it is 11 in those other three.

#### *Pusillopagurus polulus* n. sp. (Figs 25–28; Table 1)

TYPE MATERIAL. — **Holotype**. ovig ♀ 0.9 mm, Curaçao, ARMS 16, 91 m, 15.IX.2015, BCURA 0779, USNM 1297496.

**Paratypes**. Curaçao: 1 ♀ (incomplete) 0.7 mm, ARMS 13, 115.8 m, 15.IX.2015, BCURA 0632, USNM 1291925; 1 ♂ 0.7 mm, ARMS 20, 15.2 m, 15.IX.2015, BCURA 1278, USNM 1291924; 1 ovig ♀ 0.7 mm, ARMS 23, 91 m, 15.IX.2015, BCURA 1556, USNM 1291923.

**ETYMOLOGY.** — The specific name is from the Latin *polulus*, meaning small, and refers to the very small size of individuals of this new species.

**DISTRIBUTION.** — Known exclusively from Curaçao, where it has been found so far only on ARMS. Depth 15.2–115.8 m.

**HABITAT.** — Found in gastropod shells, and living in ARMS.

#### DESCRIPTION

##### *Shield (Fig. 25A)*

Subtriangular, glabrous except for scattered short setae, about as long as broad; anterior margin between rostrum and lateral projections concave; anterolateral margins sloping; posterior margin roundly truncate. Rostrum bluntly and broadly subtriangular, reaching to about same level of lateral projections. Lateral projections subtriangular, each terminating in sharp spine.

##### *Ocular peduncles*

About 0.8 length of shield, mostly glabrous or scattered short setae; corneas weakly dilated. Ocular acicles subtriangular, dorsal surface flat; terminating in bifid spine.

##### *Antennular peduncles*

Long, exceeding distal margins of cornea when fully extended by about 0.5 to 0.7 length of ultimate segment. Ultimate, penultimate and basal segments naked except for long dorsodistal seta on ultimate segment; basal segment with blunt ventromesial angle, and small spine on lateral face.

##### *Antennal peduncles*

Not exceeding distal margins of corneas when fully extended. Fifth and fourth segments unarmed except for scattered short setae. Third segment with spine on ventrodistal angle. Second segment with dorsolateral distal angle produced into spine-like process reaching slightly beyond distal margin of third segment; dorsomesial distal angle with small spine. First segment unarmed. Antennal acicles each reaching at most to about midlevel of cornea, broadly curving outward and terminating in strong spine, mesial margin with few distal setae. Flagella long, slightly exceeding tip of chelipeds, with few short setae < 1 flagellar article in length.

##### *Mouthparts*

Not dissected. Third maxilliped ischium (Fig. 25B) with crista dentata consisting of slightly projecting edge medially having three small teeth, no accessory tooth.

##### *Right cheliped (Fig. 26A, B)*

Chelipeds relatively slender, subequal in length, right not much larger. Right cheliped with moderate number of short setae or bristles. Chela elongate, ovate; fingers each terminating in sharp corneous claw overlapping when closed. Dactyl 0.7 as long as palm, lacking armature; cutting edge with two large calcareous teeth on proximal half, and uneven ridge distally; mesial margin rounded; ventral face convex, smooth. Fixed finger similar to dactyl except for cutting edge consisting of

several unequal large teeth proximally, and ridge with smaller teeth distally; dorsolateral margin weakly defined; ventral face convex, smooth. Palm long, about 1.5 times as long as broad, dorsal surface convex, with dorsomesial row of sharp, slender spines; lateral face rounded; mesial face rounded; ventral surface convex, smooth. Carpus about 1.8 times as long as broad, shorter than merus in length; dorsal surface convex, with dorsomesial row of two or three small sharp spines; lateral face rounded, mesial face flat, nearly vertical; ventral surface smooth. Merus subtriangular in cross-section; ventral face smooth, ventrolateral and ventromesial margins with distal row of two or three small spines. Ischium glabrous. Coxa with row of setae on ventromesial distal angle.

##### *Left cheliped (Fig. 26C, D)*

With moderate number of short setae or bristles. Chela elongate; fingers each terminating in sharp corneous claw slightly overlapping when closed, cutting edge of dactyl consisting of row of fused minute corneous teeth, cutting edge of fixed finger with minute calcareous teeth interspersed with fused corneous teeth. Dactyl about 1.1 times as long as palm; dorsal, mesial and ventral surfaces rounded. Palm unarmed except for dorsolateral row of small, sharp spines, mesial face rounded; ventral surface convex, smooth. Carpus about as long as merus; dorsal surface convex, with 2 or 3 minute spine or tubercles dorsomesially on distal half, and few long bristles on dorsomesial face; dorsodistal margin with 2 small spines; ventral surface convex, smooth. Merus subtriangular in cross-section; ventrolateral and ventromesial margins each with row of sharp spines. Ischium glabrous. Coxa with row of setae on ventromesial distal angle.

##### *Ambulatory legs (Fig. 27A–D)*

Exceeding tip of chelipeds when fully extended by 0.3 length of dactyls, sparsely setose. Dactyl broadly curved, about 1.6 longer than propodus, terminating in sharp, slender corneous claw; ventromesial margin unarmed or with obscure row of 2–7 very slender spinules. Propodus nearly straight; with few setae on dorsal and ventral margins, lateral and mesial faces glabrous. Carpus with small spine on dorsodistal angle, and few setae on dorsal margin. Merus somewhat laterally compressed, lateral and mesial faces glabrous, dorsal margin naked or with few setae; ventral margin with few long setae. Ischium unarmed. Anterior lobe of sternite XI (of pereopods 3; Fig. 25C) subrectangular or bilobed, distal margin with small blunt spines and fringe of setae.

##### *Fourth pereopods (Fig. 27E)*

Semichelate. Dactyl weakly curved, terminating in corneous claw, lacking preungual process; propodal rasp with single row of ovate corneous scales. Carpus unarmed except for few short setae dorsally. Merus unarmed except for with dorso-distal tuft of long setae.

##### *Fifth pereopods*

Chelate. Propodal rasp extending on dorsal surface for about 0.5 length of propodus.

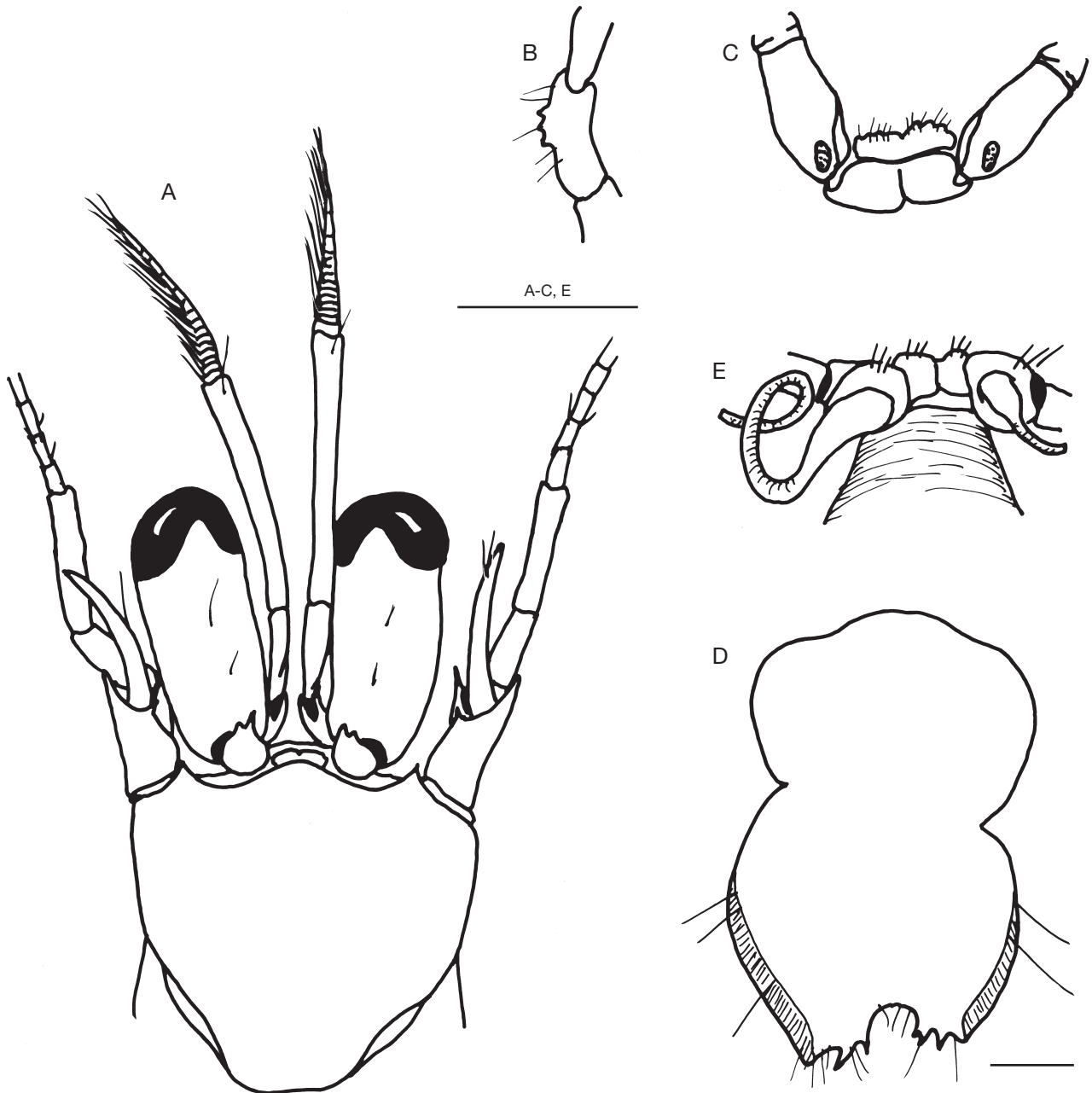


FIG. 25. — *Pusillopagurus polulus* n. gen., n. sp., Curaçao: **A–D**, holotype ovig ♀ 0.9 mm, ARMS 16, USNM 1297496; **E**, paratype ♂ 0.7 mm, ARMS 20, USNM 1291924: **A**, shield and cephalic appendages, dorsal view; **B**, ischium of left third maxilliped, internal view; **C**, sternite XI and coxae of third pereopods, ventral view; **D**, telson, dorsal view; **E**, sternite XIII and coxae of fifth pereopods with sexual tubes, ventral view. Scale bars: A–C, E, 0.5 mm; D, 0.1 mm.

#### *Uropods and telson (Fig. 25D)*

Uropods markedly asymmetrical, left largest. Telson weakly asymmetrical, about 1.5 longer than broad; posterior lobes with distinct, thin, chitinous lateral margins, separated by broad, deep, U-shaped median cleft, terminal margins weakly oblique, setose, each armed with 2 often bifid spines, and blunt laterodistal angle.

#### *Sexual tubes (Fig. 25E) and pleopods*

Males with coxae of pereopods symmetrical, right coxa with long, coiled and distally filamentous sexual tube, left coxa with short, slender, membranous sexual tube directed slightly laterally (Fig. 25E); with unpaired left pleopods 3–5. Females

with paired gonopores; with unpaired left pleopods 2–5; eggs few (8 in single ovigerous female known), large, about 0.6 mm in maximum width.

#### *Genetic data*

See Table 1.

#### *Colour (Fig. 28)*

Shield, cephalic appendages, and chelipeds mostly white, mottled with small brown or orangish parts, cheliped fingers nearly translucent. Ambulatory legs with translucent dactyls, and weak bands of white and maroon on propodi, carpi and meri.

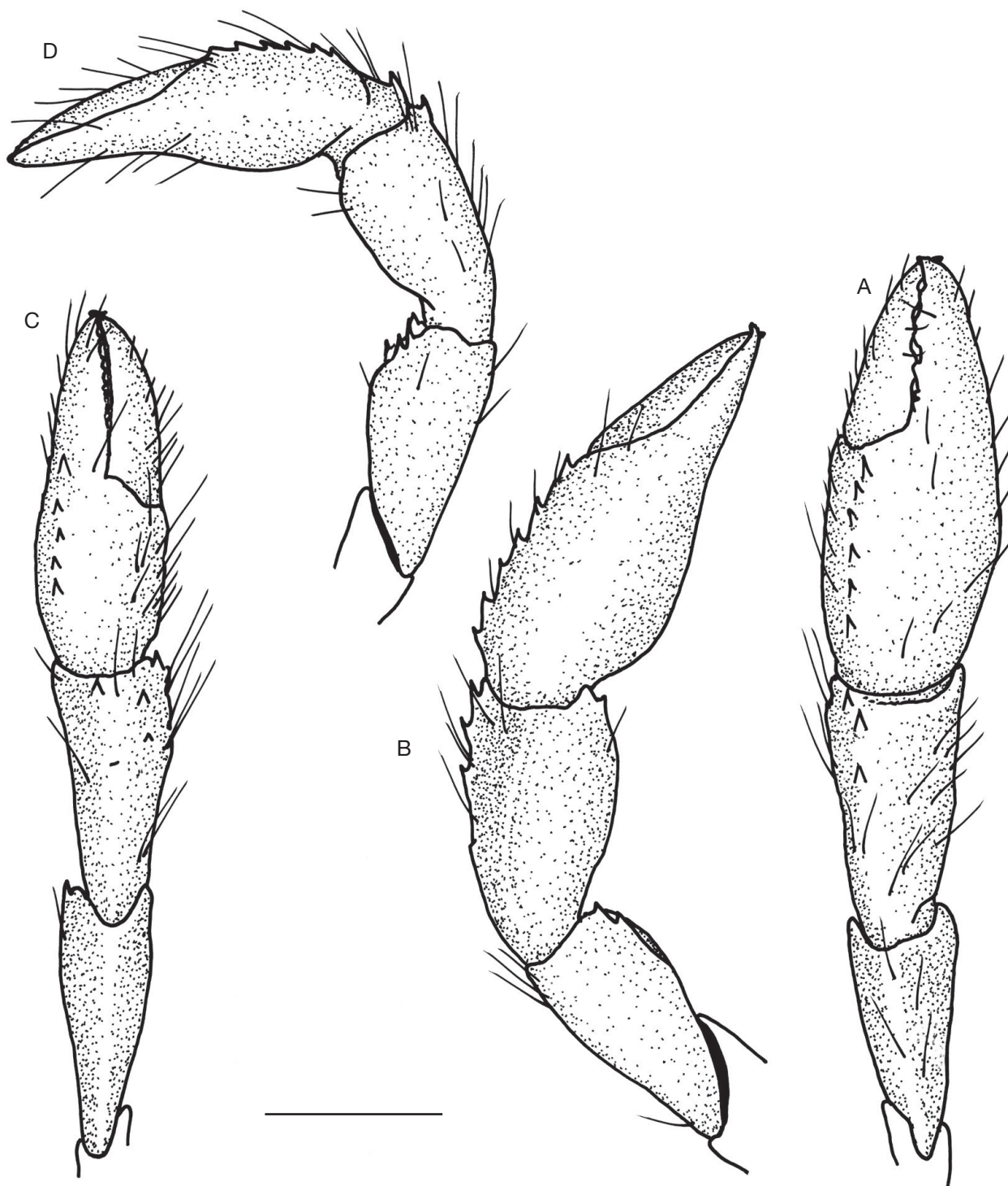


FIG. 26. — *Pusillopagurus polulus* n. gen., n. sp., holotype ovig ♀ 0.9 mm, Curaçao, ARMS 16, USNM 1297496: **A**, right cheliped, dorsal view; **B**, same, lateral view; **C**, left cheliped, dorsal; **D**, same lateral view. Scale bar: 0.5 mm.

#### REMARKS

Aside from the generic characters, this new species can be characterized by the terminal bifid ocular acicles (Fig. 25A); subequal chelipeds (Fig. 26A-D) with the right relatively slender and carpus and palm armed with dorsomesial row of sharp spines; ambulatory legs (Fig. 27A-D) with dactyls

obscurely or armed with very slender spinules on ventromesial margin; anterior lobe of sternite XI (of pereopods 3; Fig. 25C) bilobed and armed distally with small blunt spines; and telson (Fig. 25D) with relatively broad, thin, chitinous lateral margins, and terminal margins divided by broad, deep U-shaped cleft.

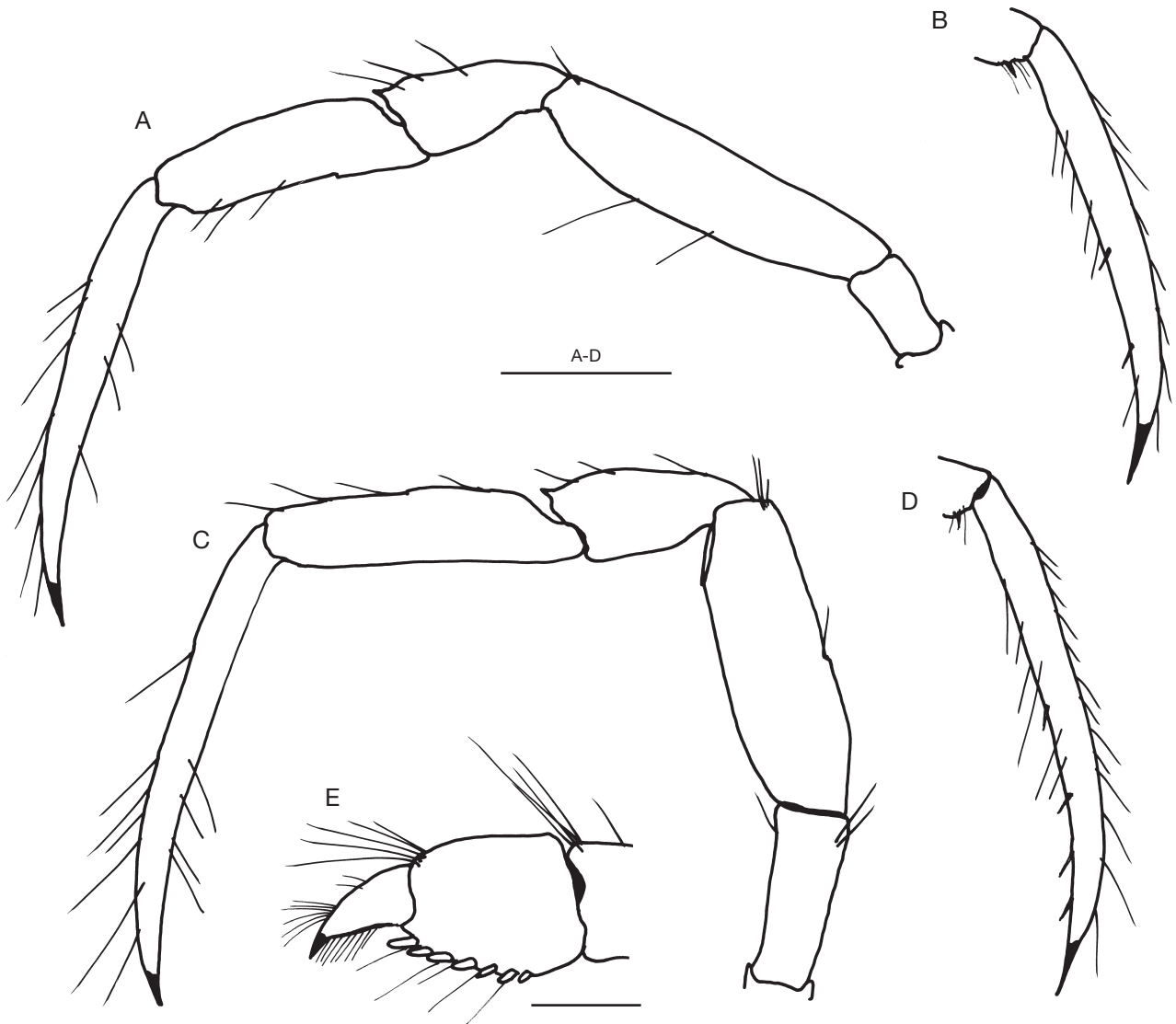


FIG. 27. — *Pusillopagurus polulus* n. gen., n. sp., holotype ovig ♀ 0.9 mm, Curaçao, ARMS 16, USNM 1297496: **A**, left pereopod 2, lateral view; **B**, dactyl of same, mesial view; **C**, left pereopod 3, lateral view; **D**, dactyl of same, mesial view; **E**, propodus and dactyl of left pereopod 4, lateral view. Scale bars: A-D, 0.5 mm; E, 0.1 mm.

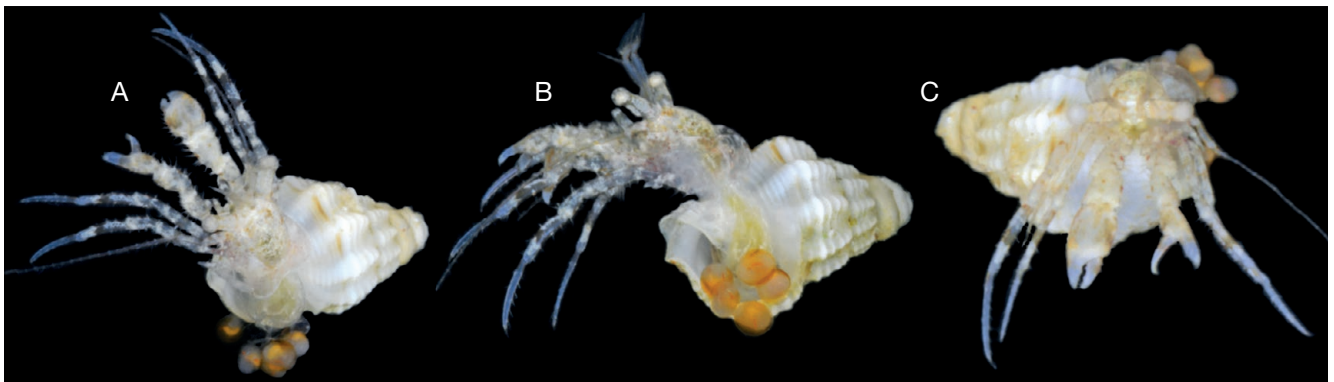


FIG. 28. — *Pusillopagurus polulus* n. gen., n. sp., Curaçao, ovig ♀ (in shell) 0.7 mm, ARMS 23, USNM 1291923: **A**, dorsal view; **B**, left lateral view; **C**, frontal view.

## DISCUSSION

## SIZE AND DIVERSIFICATION

The study of the micro-pagurid collections herein reported from Guadeloupe, Curaçao, and to some extent Dominica, has revealed a remarkable number of new genera and new species for just these three islands. These diminutive new pagurids, ranging in sl 0.4–1.5 mm, were collected in cryptic habitats, or from specialized artificial structures (ARMS) that attract a minute motile fauna that otherwise remains unseen or difficult to sample. This unexpected diversity, at such minute adult sizes and in obscure habitats, suggests that our knowledge of the pagurid fauna from the Caribbean is still inadequate and largely biased in favor of the larger species that are typically collected using coarser methods (e.g., dredging, trawling, or inshore hand-collecting). Given that the new genera and new species described herein were discovered in waters around only three among thousands of habitat rich West Indian islands of the Caribbean Sea, it is highly probable that pagurid diversity in this region remains underestimated. Furthermore, the findings of such diverse minute pagurid fauna suggests that sampling in similar habitats in other regions of the world, particularly in the habitat rich and geologically older tropical regions of the Pacific and Indian Oceans, may produce similar results, and ultimately require a recalibration of our understanding of the true richness of the pagurid fauna of the world. It is tantalizing to imagine an entire new perspective of micro-pagurid diversity (adult sl  $\leq 1.5$  mm) in general, living in the numerous cryptic, yet unstudied habitats that exist from shallow waters to deep reef structures.

## MORPHOLOGY AND EVOLUTION

The morphology of the new genera and species described herein is striking for the lack of any clear similarity or apparent close phylogenetic affinity with any of the previously known genera from the western Atlantic region, or even other regions of the world. Superficially, their morphology and use of gastropod shells as housing appears typical for pagurids, and in some cases their stout eyes and diminutive size could conduce to misinterpretation of specimens as being first crab stages or immature juveniles. Yet, it is clear that they are sexually mature adults, including ovigerous females with few (< 10 to 30) relatively large eggs ranging in maximum width from 0.3 to 0.6 mm, a condition that is known to be indicative of abbreviated development (Rabalais & Gore 1985). Examination of specimens at high magnifications reveals various unique characters on the cephalothorax, mouthparts, pereopods, ambulatory legs, thoracic sternites, telson, and secondary sexual characters, that clearly define each of the new taxa. Even color patterns observed while alive, are quite distinct. As tissue samples for genetic analyses have been obtained for most of the specimens, and raw sequence data are cited here to augment descriptions with genetic identify (Table 1), it will be of considerable interest to further explore molecular phylogenetic relationships among these new taxa.

As previously mentioned, all but one of the new species discovered, and all males in the six new genera, have sexual tubes, although none could be matched with sexual tube or other morphological conditions found in the other 11 western Atlantic pagurid genera with male sexual tubes: *Catapaguroides* A. Milne-Edwards & Bouvier, 1892, *Catapagurus* A. Milne-Edwards, 1880, *Enneobranchus* García-Gómez, 1988, *Goreopagurus* McLaughlin, 1988, *Iridopagurus* de Saint Laurent-Dechancé, 1966, *Michelopagurus* McLaughlin, 1997, *Nematopaguroides* Forest & de Saint Laurent, 1968, *Ostraconotus* A. Milne-Edwards, 1880, *Pylopagurus* A. Milne-Edwards & Bouvier, 1893, *Solenopagurus* de Saint Laurent, 1970a, and *Spathapagurus* Lemaitre & Felder, 2011. Neither could any significant similarity be found with the remaining 45 pagurid genera from other regions of the world in which the male has sexual tubes. With the description of the new genera described in this report, there are now 88 genera of Paguridae known from the world, of which 56 or 63.6% have males with sexual tubes, a high enough percentage to suggest the presence of these tubes may represent a reproductive specialization that has contributed to the evolutionary success of the family. Regrettably, knowledge of the reproductive biology and behaviour of pagurids with sexual tubes is scant at best, although recent investigations have at least begun to clarify details of the complex morphology of sexual tubes in species of various genera (Tudge & Lemaitre 2004, 2006).

Also of significance is the unusually low number of gills in five of the eight new species described herein, with only eight pairs of gills in *Paguriscus robustus* n. gen., n. sp., *Pagurus abditus* n. sp., and *Pusillopagurus polulus* n. gen., n. sp., and nine pairs in *Pagurellus jenniferae* n. gen., n. sp. and *Pagurina bifida* n. gen., n. sp. The number of gills in the other new species *Leptopagurus rhabdotus* n. gen., n. sp., *Nematopaguroides karukera* n. sp., and *Paguruncio parvulus* n. gen., n. sp., is the typical 11 pairs that are present in the majority of Paguridae. In *Pusillopagurus* n. gen., there are no gills on the third maxilliped, a rare condition among pagurids that was known until now only in *Enneobranchus* García-Gómez, 1988, *Enneopagurus* McLaughlin, 1997, and one species of *Decaphyllus* de Saint Laurent, 1968 (*D. barunajaya* McLaughlin, 1997). As noted by McLaughlin (1997), evolutionary gill loss in the Paguroidea in general is seen in the loss of pleurobranchs on pereopods 2–5, from a full complement of four present in the Pylochelidae and some diogenids, to complete loss of pleurobranchs in some Paguridae, although rarely there are cases where arthrobranchs are lost on the third maxilliped and some pleurobranchs still remain, as herein reported for *Pusillopagurus* n. gen. The reduced number of gills in the Paguroidea is considered an advanced evolutionary condition, and thus it would appear that in the new genera and species described herein such low gill number condition may be the result of some specialization. Whether or not the tendency of gill loss in micro-pagurids is a consequence of body miniaturization and/or life in the cryptic habitats where these new species have been found, remains to be studied.

## BIOGEOGRAPHY

None of the new micro-pagurid genera or species herein described have been found in waters of more than one island, except for *Leptopagurus rhabdodus* n. gen., n. sp., which was collected in Curaçao and Dominica. Given that collecting methods in Guadeloupe were drastically different from those in Curaçao and Dominica, it is possible that such exclusive distribution is only the result of sampling different habitats, and that these micro-pagurids actually range broadly across the Caribbean and other tropical or subtropical regions of the western Atlantic. However, based on the observation that females of these species all have few, large eggs and quite possibly abbreviated development with limited larval dispersal ability, it is conceivable that their distributions are indeed confined to relatively small areas or even a few islands in the Caribbean Antilles.

The genus *Nematopaguroides* Forest & de Saint Laurent, 1968, contains only two species that occur in the western Atlantic, *N. fagei* Forest & de Saint Laurent, 1968 and *N. pusillus* Forest & de Saint Laurent, 1968. However, as neither has been reported beyond Florida, the Gulf of Mexico, and Brazil, the present description of a new species provides the first record of the genus from the West Indies.

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