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Two new marine hermit crabs allied with the *Paguristes tortugae* complex (Crustacea: Decapoda: Anomura) from the western Atlantic

CATHERINE W. CRAIG[1, 2] & DARRYL L. FELDER[1]
[1]*Department of Biology and Laboratory for Crustacean Research, University of Louisiana at Lafayette, P.O. Box 42451, Lafayette, Louisiana, 70504–2451, USA.*
[2]*Corresponding author: catherine.craig1@louisiana.edu*

Abstract

A recent molecular phylogenetic analysis that focused on selected species of western Atlantic *Paguristes* Dana, 1851, *Areopaguristes* Rahayu & McLaughlin, 2010, and *Pseudopaguristes* McLaughlin, 2002 was somewhat inconclusive regarding relationships among those genera, but it revealed two new unrecognized species genetically related to members of the *Paguristes tortugae* complex. One of the new species is sister to *A. hummi* (Wass, 1955), which is readily separated from Wass' taxon by significant differences in coloration. However, no definitive characters have been found for its identification on the basis of structural morphology. A second new species is genetically sister to *P. tortugae* Schmitt, 1933, even though it was regarded in earlier literature as no more than an ecomorphic variant expressing protective coloration related to habitat substrate color. In addition to its unique coloration, subtle distinctions are evident in structural morphology. Both species are formally named with accompanying morphological and color descriptions.

Key words: Diogenidae, Paguroidea, taxonomy, Gulf of Mexico, Central America

Introduction

Diogenidae Ortmann, 1892 has historically been treated as a monophyletic family (e.g., MacDonald *et al*. 1957; McLaughlin 1983, 2002; Cunningham *et al*. 1992; McLaughlin & Lemaitre 1997; Forest & McLaughlin 2000; Ahyong & O'Meally 2004; McLaughlin *et al*. 2007, 2010; Ahyong *et al*. 2009; De Grave *et al*. 2009), whereas others argued against this hypothesis (Tudge 1995, 1997; Tsang *et al*. 2008, 2011; Bybee *et al*. 2011; Schnabel *et al*. 2011; Bracken-Grissom *et al*. 2013; Gong *et al*. 2018; Landschoff & Gouws 2018; Tan *et al*. 2018; Wolfe *et al*. 2019). Craig & Felder (2021) presented further molecular evidence against diogenid monophyly and identified three major genetic clades. One of these monophyletic subgroups, Diogenidae Clade 1, included all *Paguristes* Dana, 1851, *Areopaguristes* Rahayu & McLaughlin, 2010, and *Pseudopaguristes* McLaughlin, 2002. This suggested that Diogenidae Clade 1 represented a multi-generic complex of over 200 species (McLaughlin & Lemaitre 2020; WoRMS 2020). The three constituent genera of Diogenidae Clade 1 were once thought to be readily differentiated from each other by gill-pair number (McLaughlin 2002; Forest *et al*. 2000; Rahayu 2005, McLaughlin & Rahayu 2010), but findings of previous molecular phylogenetic analyses indicated that gill-pair number was not evolutionarily conserved within any of the three genera (Bracken-Grissom *et al.* 2013; Craig & Felder 2021). Molecular findings continue to support generally close alliance of the three genera, but the precise evolutionary relationships the generic level have remained unresolved (Bracken-Grissom *et al*. 2013; Landschoff & Gouws 2018; Craig & Felder 2021).
Despite substantial uncertainty surrounding diogenid relationships at the levels of family and genus, some historically recognized species-level morphogroups roughly correlated with clades within Diogenidae Clade 1 in recent molecular phylogenetic analyses (Bracken-Grissom *et al*. 2013; Craig & Felder 2021). One of these morphogroups, the *Paguristes tortugae* complex, originally included many western Atlantic species of *Paguristes*, several of which have been tranferred to *Areopaguristes* or *Pseudopaguristes*. In past morphological accounts, composition of the group originally included seven species, all having a characteristic fringe of setae along margins of the thoracic appendages (McLaughlin & Provenzano 1974). Originally included were the namesake of the complex, *Paguristes tortugae* Schmitt, 1933, along with *P. hewatti* Wass, 1963 (later transferred to *Areopaguristes*), *P. hernancortezi*

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McLaughlin & Provenzano, 1974, *P. angustithecus* McLaughlin & Provenzano, 1974, *P. perplexus* McLaughlin & Provenzano, 1974, *P. anomalus* Bouvier, 1918, and *P. invisisacculus* McLaughlin & Provenzano, 1974 (later transferred to *Pseudopaguristes*).

The complex has since been expanded to include several more species from the western Atlantic. Four of these, *Paguristes maclaughlinae* Martinez-Iglesias & Sanchez, 1989, *P. werdingi* Campos & Sanchez, 1995, *P. zebra* Campos & Sanchez, 1995, and *P. scarabinoi* Lima & Santana, 2017, were assigned to the complex at the time of their descriptions, based primarily on the characteristic pattern of setation. Phylogenetic analysis of available genetic data in some cases suggested the inclusion of *Areopaguristes tudgei* Lemaitre & Felder, 2012 (Bracken-Grissom *et al*. 2013; Craig & Felder 2021) and *A. hummi* (Wass, 1955) (Bracken-Grissom *et al.* 2013), although morphological arguments for these assignments were not conclusive (Lemaitre & Felder 2012). With these additions, the *P. tortugae* complex now spans a broad geographic distribution throughout the western Atlantic (Felder *et al*. 2009; Lemaitre & Tavares 2015), with constituent species found across multiple ecoregions (Spalding *et al*. 2007) from the Carolinean province on the eastern coast of North America, southwards beyond Rio de Janerio, Brazil (Table 1). Two additional previously unnamed western Atlantic species associated with the complex are herein formally described based upon morphology, coloration, and insights from DNA-based phylogenetic analyses.

TABLE 1: Type locality and geographic distribution of species of *Paguristes*, *Areopaguristes*, and *Pseudopaguristes* commonly associated with the *Paguristes tortugae* complex. Following brief descriptors, numerical designations as defined by Spalding *et al.* 2007 are given in parentheses ( ). Numbered references are listed below the table.

Species	Type Locality	Ecoregion(s) (Spalding *et al.* 2007)	Depth	References
Areopaguristes Rahayu & Mclaughlin, 2010				
A. hewatti (Wass, 1963)	Texas, USA	northern Gulf of Mexico (43)	shallow–16 m	4, 10, 12, 19
A. hummi (Wass, 1955)	Florida, USA, Franklin County	Carolinian (42), northern Gulf of Mexico (43), southern Gulf of Mexico (69), Floridian (70), Greater Antilles (65), southern Caribbean (66), southwestern Caribbean (67)	shallow–22 m	1, 3, 9, 11, 12, 13, 14, 17, 18. 19
A. rafaeli **n. sp.**	Panama, Bocas del Toro	southwestern Caribbean (67)	shallow–3 m	19
A. tudgei Lemaitre & Felder, 2012	Belize, Carrie Bow Cay	western Caribbean (68)	< 1 m	7, 19
Paguristes Dana, 1851				
P. angustithecus (McLaughlin & Provenzano, 1974)	Venezuela	southern Caribbean (66), southern Gulf of Mexico (69), Guianan (71), Amazonian (72); northeastern Brazil (75)	25–91 m	6, 10
P. anomalus Bouvier, 1918	Cuba, Fortaleza	Bermuda (62), eastern Caribbean (64), Greater Antilles (65), southern Caribbean (66), southern Gulf of Mexico (69)	< 1–63 m	1, 10, 11, 19
P. hernancortezi McLaughlin & Provenzano, 1974	Florida, Sanibel Island	Carolinean (42), northern Gulf of Mexico (43), southern Gulf of Mexico (69), Floridian (70)	55–73 m	1, 10, 13, 19
P. maclaughlinae Martinez-Iglesias & Gomez, 1989	Cuba, Isla de la Juventud	Greater Antilles (65)	603 m	5
P. perplexus McLaughlin & Provenzano, 1974	French Guiana	Greater Antilles (65), southern Caribbean (66), southwestern Caribbean (67), Guianan (71), Amazonian (72) northeastern Brazil (75)	< 1–91 m	6, 10

......*Continued on the next page*

TABLE 1 (continued)

Species	Type Locality	Ecoregion(s) (Spalding *et al.* 2007)	Depth	References
P. scarbinoi Lima & Santana, 2017	Caribbean, Uruguay	Uruguay-Buenos Aires Shelf (183)	66–68 m	8
P. tortugae Schmitt, 1933	Florida, Dry Tortugas	Carolinian (42), northern Gulf of Mexico (43), Bahamanian (63), Greater Antilles (65), southern Gulf of Mexico (69), Floridian (70), northeastern Brazil (75), eastern Brazil (76), southeastern Brazil (180)	< 1–91 m	1, 2, 5, 10, 11, 13, 14, 15, 16, 17, 18, 19, 20, 21
P. karenae **n. sp.**	Florida, Pigeon Key	northern Gulf of Mexico (43), southwestern Caribbean (67), southern Gulf of Mexico (69), western Caribbean (68), Floridian (70)	~1–41 m	10, 17, 19
P. werdingi Campos & Sanchez, 1995	Colombia, Santa Marta	southern Caribbean (66), southwestern Caribbean (67)	~20 m	3
P. zebra Campos & Sanchez, 1995	Columba, Cartegena	southern Caribbean (66), southwestern Caribbean (67)	~5 m	3
Pseudopaguristes McLaughlin, 2002				
P. invisisacculus McLaughlin & Provenzano, 1974	Florida, Ragged Key	northern Gulf of Mexico (43), Greater Antilles (65), western Caribbean (68), southern Gulf of Mexico (69)	< 1–20 m	1, 9, 10, 19

References

1. Abele & Kim 1986	7. Lemaitre & Felder 2012	13. Raz-Guzman *et al*. 1986
2. Boos *et al*. 2012	8. Lima & Santana 2017	14. Rodriguez-Almaraz *et al*. 2005
3. Campos & Sanchez 1995	9. Manjon-Cabeza *et al*. 2002	16. Soto *et al.* 1999
4. Felder 1973	10. McLaughlin & Provenzano 1974	17. Strasser & Price 1999
5. Martinez-Iglesias & Gomez 1989	11. Provenzano 1959	18. Wass 1955
6. Hernandez-Avila *et al.* 2007	12. Rahayu 2005	19. ULLZ/USNM holdings
20. Wicksten 2005	21. Soto 1980	

Material and Methods

Specimens examined were accessed from the University of Florida Natural History Museum, Gainesville, Florida, USA (UF), as well as the University of Louisiana at Lafayette Zoological Collection, Lafayette, Louisiana, USA (ULLZ), recently moved to the National Museum of Natural History, Smithsonian Institution, Washington D.C., USA (USNM). As the lengthy process of recording this transfer remains underway, both catalog numbers are used (all will be permanently cross-referenced).

Shield lengths (sl) were measured in millimeters (mm) from the tip of the rostrum to the posterior margin of the shield. All measurements were determined +/− 0.1 mm with a calibrated ocular micrometer or digital caliper. Sex and ovigerous (ov) females were noted. Collectors (coll.), are indicated for holotypes. Collection depth is shown in meters (m). Illustrations were made on a Wild M5 or Leica MZ8 dissecting microscope with a camera lucida. The resulting drawings were refined in Adobe Photoshop.

Color comparisons were made from observations of live animals and comparisons of archived digital photographs corresponding to genetic voucher specimens from ULLZ. Digital photographs were made on Nikon or Fuji Finepix cameras equipped with a 60 mm Nikon macrolens. After being briefly frozen or narcotized in clove oil, subjects were positioned below the water surface of a shallow tray lined with black felt to serve as background and were illuminated by either mirrored sunlight or 5000°K artificial lighting.

Results

Taxonomy

Family Diogenidae Ortmann, 1892

***Areopaguristes rafaeli* n. sp.**
(Figs 1D, C, 2A–G, I, 3, 4)

Areopaguristes nr. *hummi.*—Craig & Felder, 2021: table 1, 304, 311, 317.
Areopaguristes "nr. *hummi* nov. sp." — Craig & Felder, 2021: fig. 1.

Type material. **Holotype**: male DNA and photo voucher, sl 2.5 mm (ULLZ 15009/USNM 1548225), Panama, Bocas del Toro, stn. 9, by SCUBA, 3 m, 03 Aug 2004, coll. D. Felder, R. Lemaitre, and colleagues.

Paratypes: 2 males, sl 2.5, 2.3 mm (ULLZ 18007/USNM 1661768), Panama, Bocas del Toro, stn. 48, Almirante pilings, 9°16.218'N, 82°23.382'W, snorkeling, 11 Aug 2004.

Diagnosis. Twelve pairs biserial gills. Antennal flagellum short with dense setae approximately 6–8 articles in length originating on ventral surfaces. Antennular peduncles extending beyond cornea distal margins by at least 0.5 length of ultimate peduncular segment. Ocular acicles subtriangular, flushly abutted along mesial margins with numerous spines along lateral border. Rostrum obsolete. Maxillule proximal and distal endite mesial borders bearing brushes of short, finger-like setae, exopod external lobe with dorsal projection well developed. Second and third pereopod dactyli unarmed. Second pereopod propodi, carpi, and meri dorsal margins each bearing row of acute spines, many with corneous tips. Telson weakly asymmetrical, posterior lobe terminal margins well armed. Male first pleopod inferior lamella distal margin bearing single row of curved spines. In life, eyestalks uniformly golden or straw colored, cheliped merus mesial surface lacking blue markings, with distinct black crescent at distal extremity. Applicable GenBank sequence accession numbers from Craig & Felder (2021) for holotype, ULLZ 15009/USNM 1548225: (H3) MW160335; (12S) MW160980; (16S) MW167181.

Description. Twelve pairs of biserial gills. Shield (Fig. 2B) subtriangular, length slightly exceeding width. Dorsal surface central region convex, bearing widely spaced tufts of setae, most abutting spines or tubercles; lateral surface bearing widely-spaced low tubercles and small spinules; anterior margins between rostrum and lateral projections weakly concave; anterolateral angle obtuse, bearing irregularly spaced spines and spinules. Rostrum obsolete, unarmed, not extending distally beyond lateral projections. Lateral projections each bearing prominent spine and tuft of setae. Branchiostegite lateral surface with granular texture, moderately setose, with dorsal and anterior margins each bearing row of small spines. Posterior carapace poorly calcified, lateral surfaces bearing scattered setae.

Ocular peduncles (Fig. 2B) subcylindrical, narrowing slightly at mid-length, diameter at base approximately equal to that at cornea, lacking any banding, spotting, or other patterning, corneas black. Ocular acicles subtriangular; mesial margins unarmed and flushly abutted at midline; lateral margins somewhat oblique, bearing numerous small spines.

Antennular peduncles (Fig. 2B) extending anteriorly beyond cornea distal margin by approximately 0.7 times length of ultimate segment; ultimate segment dorsal surface with row of minute setae; basal segment lateral surface bearing minute spine, distolateral angle bearing spine; flagellum secondary (ventral) ramus well developed.

Antennal peduncles (Fig. 2B) extending anteriorly slightly beyond cornea distal margin. Fifth segment without remarkable characteristics. Fourth segment dorsodistal angle bearing small spine, easily obscured by antennal acicle from dorsal view. Third segment ventromesial distal angle bearing acute spine; ventral margin sparsely setose. Second segment dorsolateral distal angle bearing acute spine; dorsomesial distal angle likewise. First segment unarmed. Antennal acicles extending anteriorly slightly beyond 0.5 distal length of ocular peduncles; lateral margin unarmed and sparsely setose; mesial margin oblique, bearing numerous spines and short setae. Antennal flagellum short, not extending beyond chelae fingertips, densely setose, setae approximately 6–8 articles in length and originating on ventral surface of articles.

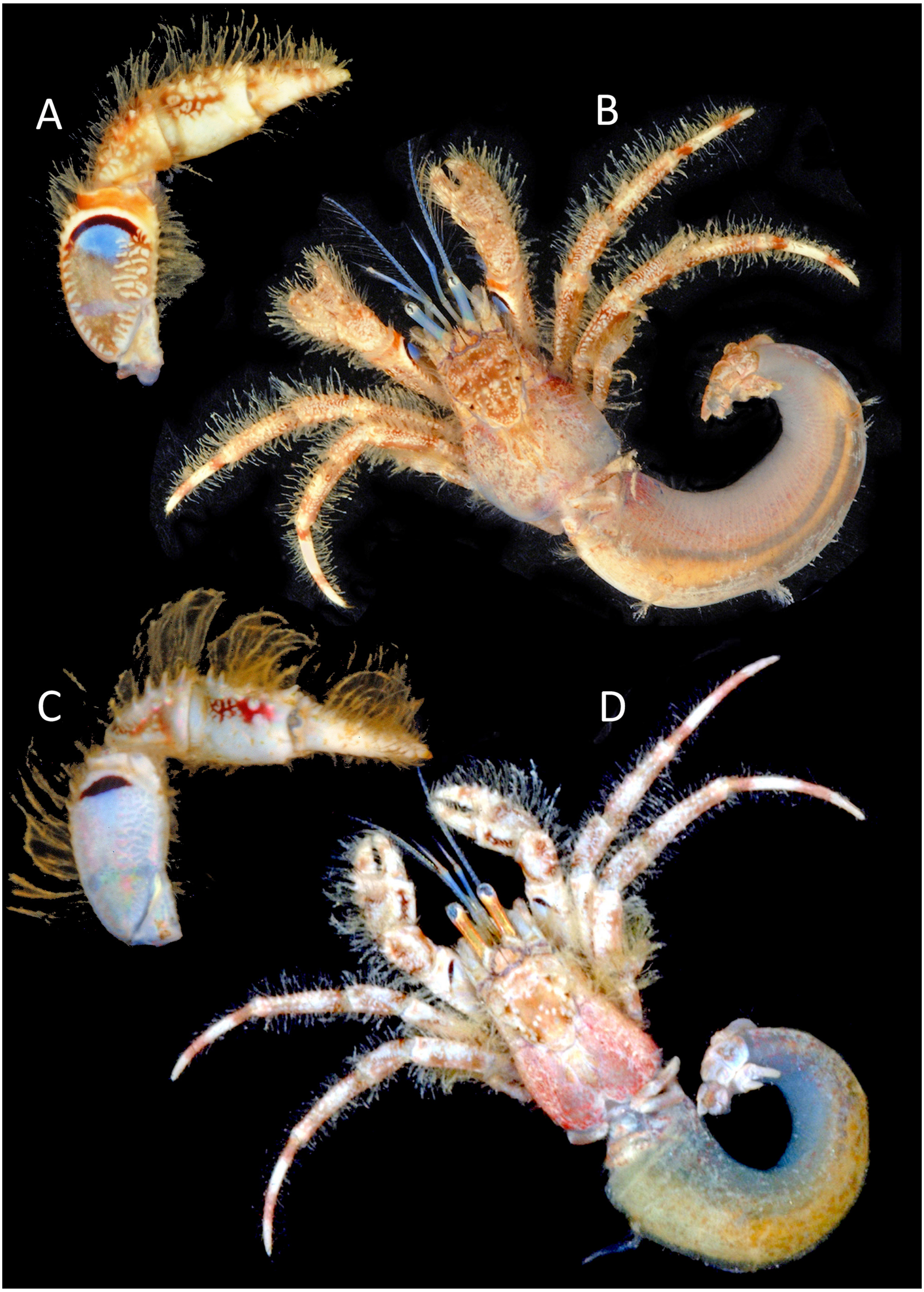

FIGURE 1. Color patterns of *Areopaguristes hummi* s.s., A, B, female, sl 3.2 mm, (ULLZ 13232/USNM 1546831), northwestern Gulf of Mexico; A, left cheliped merus, mesial surface; B, habitus, dorsal surface. *Areopaguristes rafaeli* **n. sp.**, C, D, male, sl 4.2 mm (ULLZ 15009/USNM 1548225), Panama, southwestern Caribbean; C, left cheliped, mesial surface; D, habitus, dorsal surface.

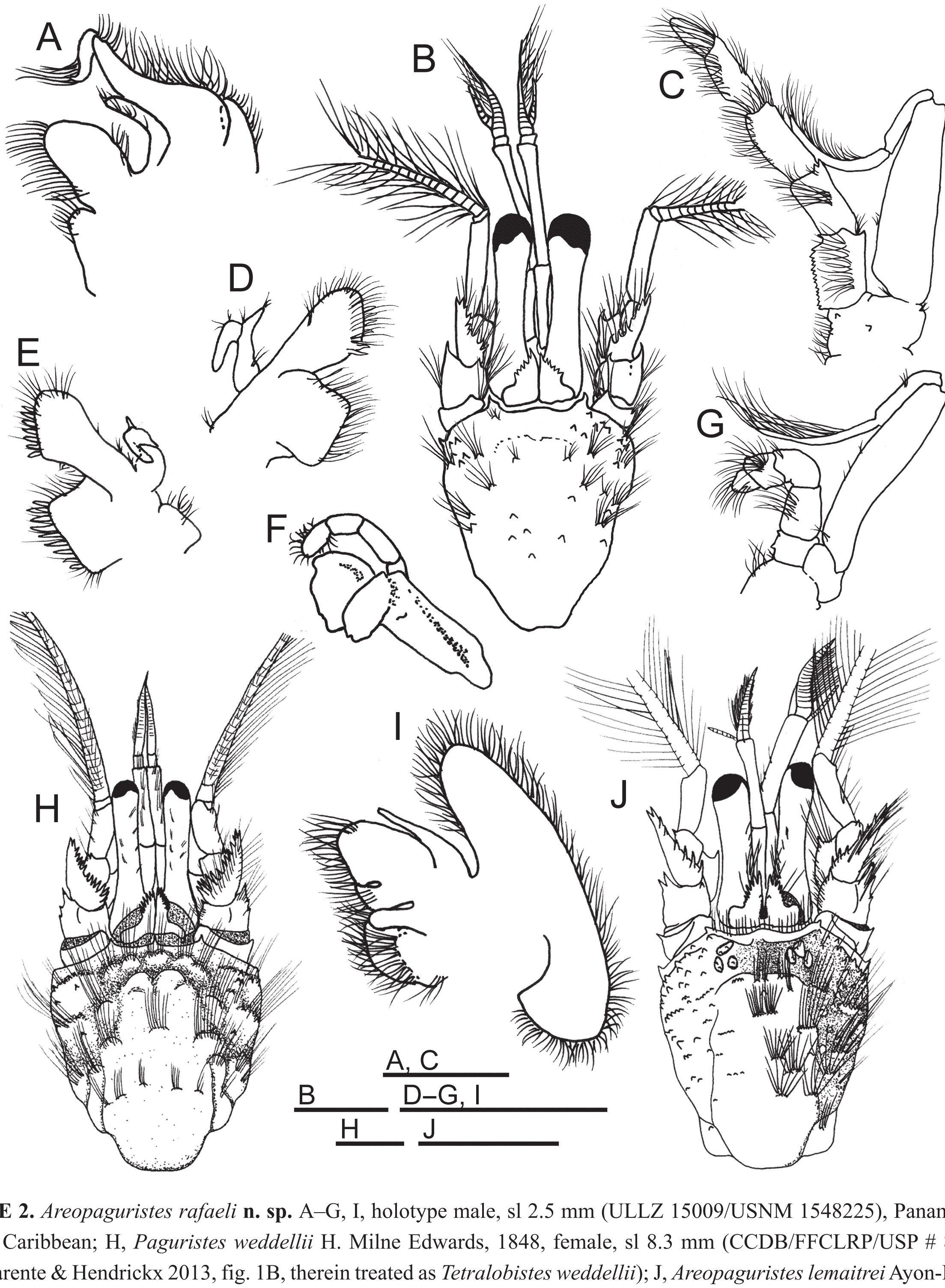

FIGURE 2. *Areopaguristes rafaeli* **n. sp.** A–G, I, holotype male, sl 2.5 mm (ULLZ 15009/USNM 1548225), Panama, southwestern Caribbean; H, *Paguristes weddellii* H. Milne Edwards, 1848, female, sl 8.3 mm (CCDB/FFCLRP/USP # 809, after Ayon-Parente & Hendrickx 2013, fig. 1B, therein treated as *Tetralobistes weddellii*); J, *Areopaguristes lemaitrei* Ayon-Parente & Hendrickx, 2012, holotype male, sl 3.40 mm (EMU-9520, after Ayon-Parente & Hendrickx 2012, fig. 1A); A, right first maxilliped, internal surface; B, carapace shield and head appendages, dorsal surface; C. right third maxilliped, internal surface; D, right maxillule, external surface; E, right maxillule, internal surface; F, right mandible, internal surface; G, right second maxilliped, internal surface; H, carapace shield and head appendages, dorsal surface; I, right maxilla, internal surface; J, carapace shield and head appendages, dorsal surface. Scale bars = 1.0 mm (A–J).

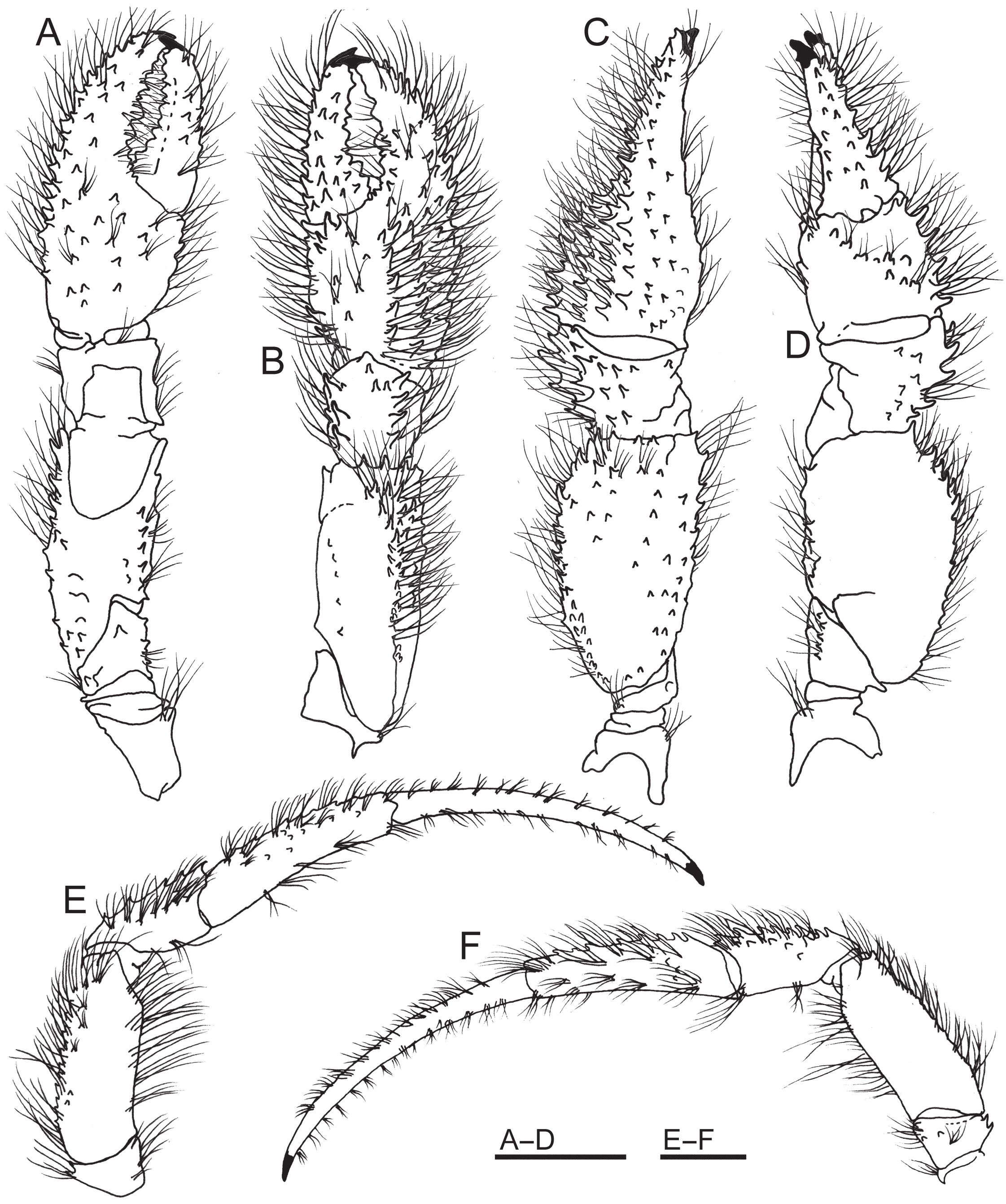

FIGURE 3. *Areopaguristes rafaeli* **n. sp.** A–F, holotype male, sl 2.5 mm (ULLZ 15009/USNM 1548225), Panama, southwestern Caribbean. A, right cheliped, ventral surface; B, right cheliped, dorsal surface; C, right cheliped, lateral surface; D, right cheliped, mesial surface; E, right second pereopod, lateral surface; F, right second pereopod, mesial surface. Scale bars = 1.0 mm (A–F).

Mandible (Fig. 2F) with incisor edge calcareous; ultimate segment of palp relatively narrow, length shorter than combined length of penultimate and basal segments. Maxillule (Fig. 2D, E) with proximal and distal endite mesial margins bearing robust, finger-like setae interspersed with fine, hair-like setae; endopod internal lobe distal angle with dorsal projection well developed (Fig. 2D), external lobe sharply recurved, length approximately 0.7 times that of internal lobe, margins of both lobes bearing scattered setae. Maxilla (Fig. 2I) proximal and distal endite mesial margins densely setose; endopod tapered distally, not overeaching distal apex of scaphognathite; scaphognathite recurved, margins densely setose. First maxilliped (Fig. 2A) endopod length approximately 0.7 times that of exopod; exopod tapering distally; epipod well developed. Second maxilliped (Fig. 2G) endopod basis bearing sparse small spinules. Third maxilliped (Fig. 2C) endopod merus internal surface with distomesial angle bearing acute spine, external surface bearing small spine at midline; ischium with crista dentata well developed, lacking accessory tooth.

Chelipeds (Fig. 3A–D) subequal in size, similarly armed, fingers opening transversely, tips slightly crossed; dorsal surfaces of chelae and carpi densely covered with tufts of plumose setae partially obscuring armature beneath, longer setae forming dense fringe along dorsolateral and dorsomesial margins of chelae, and carpus; fixed and moveable finger each terminating in tapered corneous tip. Dactyl length approximately 3 times maximum height; cutting edge bearing calcareous teeth and widely spaced tufts of stiff bristles; dorsal surface bearing irregularly spaced spines, most abutting tuft of setae; dorsomesial margin bearing irregular row of corneous-tipped spines decreasing in size distally, most abutting tuft of setae; mesial surface bearing irregular row of conical spines continuing distally as unevenly spaced small tubercles, most abutting tufts of setae. Fixed finger not extending beyond cheliped dactyl; cutting edge bearing calcareous teeth bordered with row of stiff bristles ventrally. Palm dorsal surface somewhat convex; dorsolateral surface bearing 2 irregular longitudinal rows of strong spines, each spine abutting tuft of setae; dorsolateral margin bearing longitudinal row of spines continuing onto fixed finger lateral margin; ventral surface bearing widely spaced tubercles, spines, and tufts of setae; lateral surface bearing irregular, longitudinal row of spines interspersed with tufts of short setae; mesial surface slightly convex, bearing shallow rugae and small tubercles. Carpus length approximately 0.3 times that of chela; dorsal surface bearing scattered conical spines and spinules interspersed with setae; dorsolateral and dorsomesial margins well defined and slightly elevated, each bearing row of corneous-tipped spines; dorsolateral surface bearing evenly spaced spines; mesial surface bearing scattered small tubercles and spines. Merus length approximately 2.5 times that of carpus, subtriangular in cross section; dorsal margin bearing small tubercles proximally, as well as dense cluster of conical spines and spinules distally, some with corneous tips, ultimate distal margin bearing widely spaced spines; ventromesial margin bearing unevenly spaced, irregular spines; lateral surface bearing irregularly spaced spines ventrally; ventrolateral margin with row of conical spines increasing in size distally. Ischium ventromesial margin bearing row of blunt spinules and scattered setae. Coxa ventrodistal angle with dense tuft of setae visible in mesial view.

Second pereopod (Fig. 3E, F) slender, extending beyond cheliped by approximately 0.5 length of second pereopod dactyl; dorsal and ventral margins of dactyl, propodus, carpus and merus bearing dense fringe of setae. Dactyl subcylindrical, length as much as 10 times maximum height, curved ventrally from lateral view and terminating in curved corneous claw; dorsal and ventral margins unarmed, bearing widely spaced tufts of setae; mesial and lateral surfaces likewise. Propodus length approximately 0.7 times that of dactyl; dorsal margin armed with slender spines decreasing in size distally (in mesial view); ventral margin unarmed; dorsolateral surface bearing widely spaced low tubercles, some abutting tufts of setae; mesial surface bearing scattered small tubercles and widely spaced tufts of setae. Carpus length approximately 0.5 times that of propodus; dorsal margin bearing row of irregularly spaced spines (in mesial view); ventral margin unarmed; lateral surface (Fig. 3E) moderately convex, dorsolateral surface with slight longitudinal ridge bearing low tubercles abutting tufts of setae; dorsomesial surface bearing sparse small tubercles and tufts of setae. Merus length approximately 2 times that of carpus, somewhat laterally compressed; dorsal margin bearing irregular tubercles and spines abutting tufts of setae; lateral surface bearing prominent tubercle abutting dense tuft of setae distally; dorsolateral surface bearing irregularly spaced, small tubercles and scattered tufts of setae. Ischium laterally compressed, mesial and lateral surfaces subtriangular, dorsodistal angle bearing prominent spines. Coxa without distinguishing characters.

Third pereopod (Fig. 4A, B) similar in proportions and armature to second pereopod except as noted. Propodus length approximately 8 times that of dactyl; dorsal margins lacking distinct spines or spinules. Carpus dorsal margin unarmed except for small spine at dorsodistal angle; lateral surface longitudinal ridge less prominent than that of second pereopod. Merus length approximately 1.5 that of carpus; dorsal margin lacking distinct spines or spinules. Ischium length approximately 0.5 times that of merus; mesial and lateral surfaces subrectangular; dorsolateral surface bearing irregularly spaced minute tubercles. Sternite of third pereopod with anterior lobe subrectangular, bearing rounded tubercles with dense tufts of setae.

Fourth pereopod (Fig. 4D) not extending beyond distal margin of third pereopod merus, segments somewhat laterally compressed; propodus, carpus, and merus dorsal margins bearing dense fringe of long setae. Dactyl (Fig. 4E) terminating in elongate corneous claw abutting dense tuft of bristles dorsally; distoventral margin bearing 2 (in holotype) acute spines abutting preungual process. Preungual process well-developed, slender, length slightly less than that of corneous claw. Propodus length approximately 2 times that of dactyl; ventrolateral surface bearing narrow propodal rasp extending approximately 0.3 length of segment. Carpus, merus, and ischium/basis similar in length, dorsal and ventral margins of each bearing dense fringe of setae. Coxa distal margin with fringe of stiff setae; ventromesial surface with row of minute spines interspersed with setae.

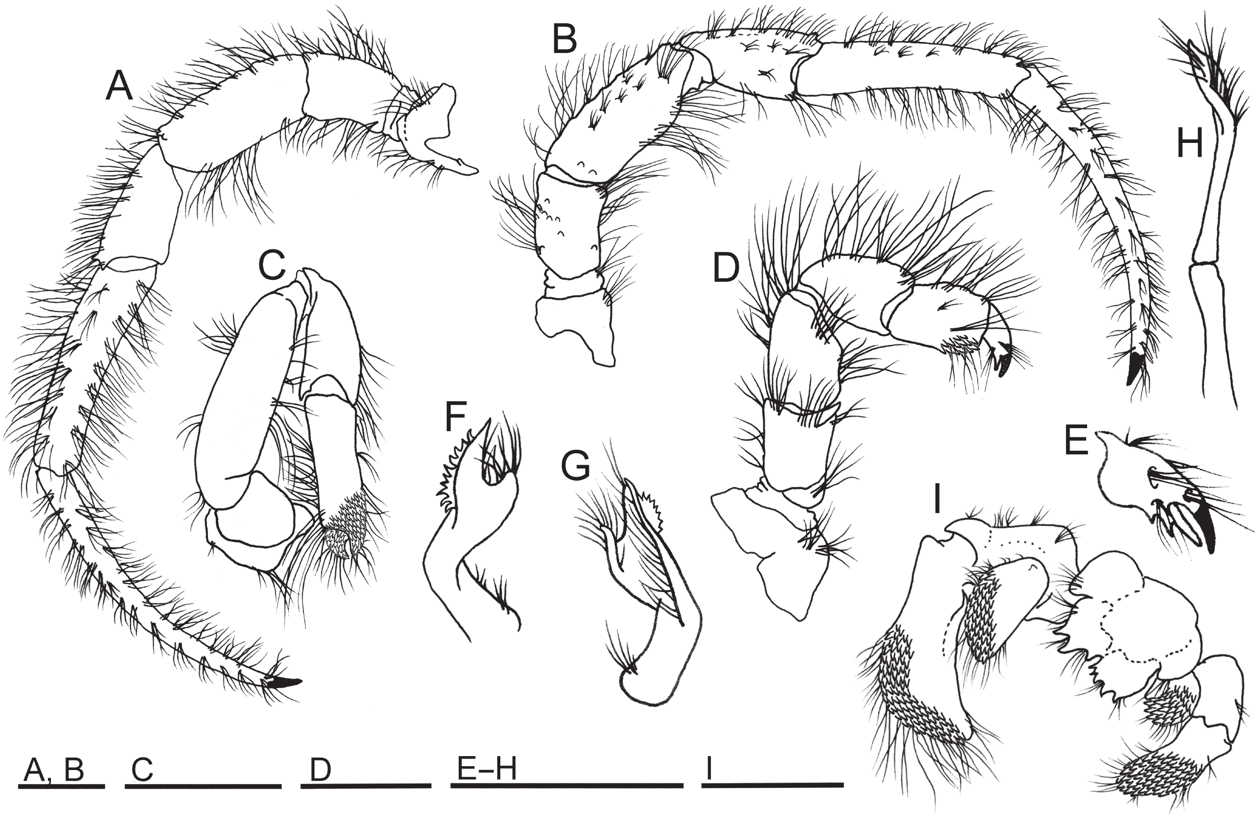

FIGURE 4. *Areopaguristes rafaeli* **n. sp.** A–I, holotype male, sl 2.5 mm (ULLZ 15009/USNM 1548225), Panama, southwestern Caribbean. A, right third pereopod, mesial surface; B, right third pereopod, lateral surface C, right fifth pereopod, lateral surface; D, right fourth pereopod, lateral surface; E, right fourth pereopod dactyl; F, right first pleopod, mesial surface; G, right first pleopod, internal surface; H, right second pleopod; I, telson and uropods, dorsal surface. Scale bars = 1.0 mm (A–I).

Fifth pereopod (Fig. 4C) chelate; fixed finger subequal in length to dactyl; appendage segments generally subcylindrical. Propodus elongate, length approximately 3 times maximum height; lateral surface bearing rasp continuous across dactyl, fixed finger and approximately 0.3 distal length of segment; ventromesial surface concave, bearing dense patch of setae distally.

Abdomen curled, poorly sclerotized. Male first (Fig. 4F, G) and second (Fig. 4H) pleopods each paired and modified as gonopods; pleopods 3–5 unpaired, uniramous. Male first pleopod inferior lamella lateral margin fringed with setae, distal margin with single row of curved spines; internal lamella narrow and somewhat reduced, distal margin bearing tuft of long setae; external lamella extending slightly beyond inferior lamella distal margins; second pleopod (Fig. 4H) ultimate segment terminal lobe somewhat deflected laterally and densely setose.

Uropods (Fig. 4I) strongly asymmetrical, left robust and elongate. Telson (Fig. 4I) weakly asymmetrical (in holotype); left lobe somewhat longer than right, deep lateral incisions dividing anterior and posterior portions; anterior lobes subovate; posterior lobes subtriangular to subquadrate, left and right separated by well-defined cleft, left lobe terminal margin bearing prominent conical spines with corneous tips, curving outward somewhat, right lobe bearing smaller, irregular spines, some with corneous tips.

Size. Largest examined, male, sl 2.5 mm

Color. (Fig. 1C, D). Pale buff or peach background color marked with irregular orange to rust patches over cheliped and carapace shield. Walking legs bearing irregular orange to rust banding on propodus, carpus, and merus. Second and third pereopod dactyls each bearing two distinct orange to rust bands alternating with white. Cheliped merus mesial surface bearing black, crescent shaped marking at distal extremity and lacking any blue markings. Eyestalks solid golden yellow, lacking any bands, stripes, or spotting.

Etymology. The species name, “rafaeli”, honors our colleague and friend, Rafael Lemaitre, for his many contributions to studies of paguroid and other decapod crustaceans, as well as his assistance in field collections and valuable editorial advice that facilitated the present project.

Distribution and habitat. So far known only from the type series, *A. rafaeli* **n. sp.** is found near Bocas del Toro, Panama, in the southwestern Caribbean and has been collected in shallow water approximately 3 m deep.

Morphological variations. In general, smaller paratypes show reductions in the number and prominence of spines on the thoracic appendages and telson terminal margins. This is especially evident on the dorsal surfaces of the chelae and carpus. Accompanying this variation, the number of spines abutting the preungular process of the fourth pereopod is reduced from two to one when our smallest male (sl 2.1 mm) is compared to our largest, the holotype male (sl 2.5 mm). For the ocular acicles, the mesial margins are always unarmed and flushly abutted at the midline, although the lateral margin shape can range from straight and oblique as in the holotype male (Fig. 2B), to fan-shaped in the smaller paratypes, resembling more closely what is provisionally the generic type of *Paguristes* (see Craig & Felder 2021: 301–302), *Paguristes weddellii* H. Milne Edwards, 1848 (Fig. 2H) or *Areopaguristes lemaitrei* (Fig. 2J). However, the most notable variation among paratypes is in the shape of the telson, which shows higher degrees of asymmetry in the smaller individuals.

Remarks. In addition to molecular genetic and coloration characters that separate *Areopaguristes rafaeli* **n. sp.** from its sister species, *A. hummi*, the two species appear to be well-separated in range. So far, the known occurrence of our new species is restricted to a small area of the Caribbean coast, while *A. hummi* is recorded from many localities in the Gulf of Mexico (Table 1). Differences in color between the new species and *A. hummi* are very evident in life, especially in pigmentation and patterning of the cheliped merus, eyestalks, and cephalic appendages. The latter species (Fig. 1A, B) is readily recognized by the prominent blue spot upon the cheliped merus mesial surface that is bordered along the distal edge by a black semicircular band (Fig. 1A), whereas this new species (Fig. 1C, D) lacks the blue meral spot, and the semicircular black band at the distal margin of the merus mesial surface is reduced to a black crescent-shaped marking (Fig. 1C). As confirmed via photographic records, the eyestalks, antennular peduncles, and antennal flagella of *A. hummi* are predominantly solid blue in color (Fig. 1B). This coloration of the cephalic appendages and eyestalks definitively sets *A. hummi* apart from *A. rafaeli* **n. sp.**, which has light orange to straw-colored eyestalks, likewise confirmed through photographic documentation (Fig. 1D). However, no definitive characters based on structural morphology are known to separate the two species.

In addition to its striking morphological similarity to *Areopaguristes hummi*, the new species shares several general characteristics with other species of *Areopaguristes* and the *P. tortugae* complex (Table 2). However, as suggested by genetic evidence (Craig & Felder 2021), the treatment of *A. hummi* and its closest genetic allies as closely related to the *P. tortugae* complex may not be warranted, and morphological characters offer conflicting support. Favoring their inclusion in the *P. tortugae* complex, *A. hummi*, *A. rafaeli* **n. sp.**, and their nearest genetic associates exhibit the characteristic fringe of setae on the thoracic appendages, an armed telson, and spines on the male gonopod external lobe inferior lamella. As with all other members of the complex, both *A. hummi* and *A. rafaeli* **n. sp.** bear an epipod on the first maxilliped. This epipod is likewise present in the generic type species *A. setosus* (H. Milne Edwards, 1848) (see Rahayu 2005), but recent emendments to the generic diagnosis based on evaluations of *A. oxyophthalmus* (Holthuis, 1959) and *A. praedator* (Glassell, 1937) assert that the presence of the first maxilliped epipod is not diagnostic at the genus level (Ayon-Parente *et al*. 2015). The full significance of variability in this character across the presently accepted membership of *Areopaguristes* remains unexplored, but the presence or absence of the first maxilliped epipod is so far diagnostic at the species level and shows potential utility in the designation of *Areopaguristes* subgroups, or perhaps even future generic diagnoses.

Casting doubt on the affinity of *Areopaguristes hummi* and *A. rafaeli* **n. sp.** with other *P. tortugae* complex constituents, the pereopods of *A. hummi* and its genetic allies are slender and generally subcylindrical with the proportions of the pereopod segments, especially the elongate nature of the dactyl, drastically different from those of *P. tortugae* and its genetic allies such as *A. hewatti*. Additionally, the ocular acicles of *A. hummi* and *A. rafaeli* **n. sp**. are greatly dissimilar in shape and orientation from those of other species currently considered members of the *P. tortugae* complex. Being flushly abutted at the midline and accompanied by a greatly reduced rostrum, the configuration most closely resembles that of a handful of eastern Pacific species including *A. lemaitrei* Ayon-Parente & Hendrickx, 2012 (Fig. 2J), *A. waldoschmitti* Ayon-Parente & Hendrickx, 2012, and *P. weddellii* (Fig. 2H). Further, for *A. hummi* and *A. rafaeli* **n. sp.**, the gonopod (Fig. 4G, H) in males is shorter and stouter than that of most other species of *Paguristes* and *Areopaguristes* from the western Atlantic, aside from *A. tudgei*.

TABLE 2: Summary of diagnostic morphological characters for species commonly regarded as comprising the *Paguristes tortugae* complex.

Species	acicles	rostrum	setae of antennal flagellum	antennule length	eyestalk shape	eyestalk patterning	brood pouch	male gonopod inferior lamella	female first pleopods
Areopaguristes									
A. hewatti	widely separated	exceeding lateral projections; acute tip	1–3 articles in length	not exceeding corneas	subcylindrical; slightly narrowed at midlength	banded near midlength	large; subovate	armed	present; paired
A. hummi	flushly abutted	obsolete	6–8 articles in length	exceeding corneas	subcylindrical; slightly narrowed at midlength	solid blue	absent	armed	absent
A. rafaeli **n. sp.**	flushly abutted	obsolete	6–8 articles in length	exceeding corneas	subcylindrical; slightly narrower at midlength	solid, straw colored	unconfirmed	armed	not established
A. tudgei	widely separated	exceeding lateral projections; acute tip	1–3 articles in length	slightly exceeding cornea	subcylindrical; greatly swollen at base	distally solid blue	absent	unarmed	present; paired
Paguristes									
P. angustithecus	widely separated	exceeding lateral projections; acute tip	6–8 articles in length	equal to or exceeding corneas	subcylindrical; slightly narrowed at midlength	banded near midlength	elongate; blade shaped	armed	present; paired
P. anomalus	widely separated	exceeding lateral projections; rounded	1–3 articles in length	not exceeding corneas	subcylindrical; bulbous base	distally solid blue	absent	armed	present; paired
P. hernancortezi	widely separated	exceeding lateral projections; acute tip	1–3 articles in length	not exceeding corneas	subcylindrical; slightly narrowed at midlength	spotted; somewhat translucent	small; subquadrate	armed	present; paired
P. maclaughlinae	widely separated	not exceeding lateral projections; rounded tip	1–3 articles in length	greatly exceeding corneas	subcylindrical slightly swollen at base	patterning absent in preservation	large; subquadrate	armed	not established
P. perplexus	widely separated	exceeding lateral projections; acute tip	1–3 articles in length	not exceeding corneas	subcylindrical; slightly narrowed at midlength	dark bands at midlength	subtriangular	armed	present; paired
P. scarabinoi	widely separated	exceeding lateral projections; acute tip	6–8 articles in length	not exceeding corneas	subcylindrical; slightly narrower at midlength	patterning absent in preservation	elongate; blade shaped	armed	present; paired

......*Continued on the next page*

TABLE 2: (continued)

Species	acicles	rostrum	setae of antennal flagellum	antennule length	eyestalk shape	eyestalk patterning	brood pouch	male gonopod inferior lamella	female first pleopods
P. tortugae	widely separated	exceeding lateral projections; acute tip	1–3 articles in length	not exceeding corneas	subcylindrical; slightly narrowed at midlength	banded at midlength	large; subovate to subquadrate	armed	present; paired
P. karenae **n. sp.**	widely separated	exceeding lateral projections; acute tip	1–3 articles in length	not exceeding or exceeding corneas	subcylindrical; slightly narrowed at midlength	banded at midlength	large; subovate to subquadrate	armed	present; paired
P. werdingi	widely separated	exceeding lateral projections; acute tip	1–3 articles in length	not exceeding corneas	subcylindrical; bulbous base	distally solid blue	absent	armed	present; paired
P. zebra	widely separated	exceeding lateral projections; acute tip	1–3 articles in length	not exceeding corneas	subcylindrical; slightly narrowed at midlength	irregular dark bands along length	large; subovate to subquadrate	armed	present; paired
Pseudopaguristes									
P. invisisacculus	widely separated	exceeding lateral projections; acute tip	1–3 articles in length	not exceeding corneas	subcylindrical; slightly narrowed at midlength	distally solid blue	subtriangular	armed	present; paired

***Paguristes karenae* n. sp.**
(Figs 5B, 6–8)

Paguristes tortugae.—Provenzano, 1959: 389, 392 (part, green carapace with red spines on cheliped carpus and manus inner margins), fig. 11A; Williams, 1965: 115, 119 (part, green carapace with red spines on cheliped carpus and manus inner margins, not fig. 96); McLaughlin & Provenzano, 1974 (part, "darker forms"); Williams, 1984: 205, fig. 144 (USNM 151492); Wicksten, 2005: 34, table 1 (part, uncertain identification suggested, footnote 20); Venera-Pontón *et al*., 2020, 4, table 1 (part, ULLZ 13663, 13665, 13707, 13708).
Paguristes sp.—Strasser & Price, 1999: 34, 41.
Paguristes nr. *tortugae*.—Craig & Felder, 2021: table 1, 307, 311, 316, 317.
Paguristes "nr. *tortugae* nov. sp.".—Craig & Felder, 2021: fig. 1, 312

Type material. Holotype: male DNA and photo voucher, sl 5.6 mm (ULLZ 4782/USNM 1540546), Florida Keys, Pigeon Key, Florida, 09 June 2001, coll. K. Strasser (Barkel).

Paratypes: *Florida Atlantic coast and Keys:* 1 female photo voucher, sl 3.2 mm (ULLZ 5647/USNM 1542520), off Ft. Pierce, Florida, 15m, 09 Sep 2003; 1 male photo voucher, sl 6.1 mm, 1 male, sl 3.4 mm (ULLZ 12171/USNM 1546239), Big Pine Key, Boogie Canal, scallop dredge, 2–3 m, 07 Jul, 1979; 1 male photo voucher, sl 6.3 mm (ULLZ 15244/USNM 1548287) Content Keys, dredge, 2–4 m, 27 Jun 1984; 1 male photo voucher, sl 5.6 mm, 1 male, sl 4.3 mm (ULLZ 15245/USNM 1548289), Big Pine Key, Newfoundland Harbor, dredge, 2–4 m, 25 Jun 1984; 1 male DNA voucher, sl 5.9 mm (UF 015380), Tampa Bay, 4 km West of Sunshine Skyway, spoil heap with sponges, 6–7 m, 07 Feb 2009.

Northeastern Gulf of Mexico: 2 males, DNA and photo vouchers, sl 3.9, 4.9 mm (ULLZ 8578/USNM 1543769), cruise NSF-III-055, 28°10.28'N, 84°1.95'W, 41 m, 04 Jul 2006.

Belize. 1 female DNA and photo voucher, sl 3.0 mm, 1 female sl 2.0 mm (ULLZ 11116/USNM 1545590), Twin Cays, rubble, 20 Feb 2009; 1 male photo voucher, sl 4.2 mm (ULLZ 3563/USNM 1540063), Carrie Bow Cay, 1 m, 20 Apr 1983.

Panama (Caribbean): 1 ov female DNA voucher, sl 3.4 mm (ULLZ 13664/USNM 1547025), Bocas del Toro, 09°21.060'N, 82°15.540'W, grass beds and *Porites*, 2 m, 08 Aug 2011; 1 male DNA voucher, sl 4.7 mm (ULLZ 13663/USNM 1547024), Bocas del Toro, 09°21.060'N, 82°15.540'W, grass beds and *Porites*, 2 m, 08 Aug 2011; 1 male DNA voucher, sl 4.2 mm (ULLZ 13665/USNM 1547026), Bocas del Toro, 09°21.060'N, 82°15.540'W, grass beds and *Porites*, 2 m, 08 Aug 2011; 1 male DNA and photo voucher, sl 3.60 mm, (ULLZ 16969/USNM 1665635), Bocas del Toro, stn. 8, Almirante pilings, 9°16.218'N, 82°23.382'W, SCUBA, 1.5 m, 03 Aug 2004; 1 male DNA and photo voucher, sl 3.80 mm, (ULLZ 16975/USNM 1665638), Bocas del Toro, stn. 19, 05 Aug 2004; 1 male DNA and photo voucher, sl 2.60 mm (ULLZ 13330/USNM 1546874), Bocas del Toro, 07 Aug 2011; 1 male DNA and photo voucher, sl 3.6 mm (ULLZ 11743/USNM 1545935), Bocas del Toro, stn. 36, Cayo Adriana, 9°14.456'N, 82°10.413'W, 09 Aug 2004; 1 male photo voucher, sl 3.75 mm, (ULLZ 16976/USNM 1665637), Bocas del Toro, stn. 35, Bastimentos, 9°21.052'N, 82°15.340'W, 06 Aug 2004.

Other material: *Florida Atlantic coast and Keys*: 1 female photo voucher, sl 3.0 mm (ULLZ 469/USNM 1542655), 2 km southeast of St. Lucie Inlet, 0.7–10 m, 26 June, 1979; 1 ov female, sl 4.0 mm (UF 031583) Big Bend area, northwest of St. Petersberg, hard bottom, sponge reef, 29–30 m, 23 May 2012; 1 male, sl 3.3 mm (ULLZ 17737/USNM 1665636), Florida Bay, Rabbit Key Basin, 09 Dec 1998; 2 ov females, sl 3.8, 3.9 mm, 2 males, sl 4.5, 3.5 mm (ULLZ 11544/USNM 1545758), Florida Bay, eastern Rabbit Key Basin, *Thalassia* beds, 1.5 m, 22 Jul 1999; 1 male, sl 4.1 mm (ULLZ 14019/USNM 1547351), Big Pine Key, coral heads, 0.6–6 m, 03 Jul 1979; 1 ov female, sl 5.2 mm (ULLZ 9859/USNM 1544679), Looe Key area XI, 24°32.910'N, 81°24.355'W, gorgonian reef, rubble and sponges, SCUBA, 6–7 m, 22 Jun 1984.

Southwestern Gulf of Mexico: 4 males, sl 3.68, 4.55, 4.00, 3.25 mm, 1 female, sl 4.05 mm (ULLZ 11745/USNM 1545937), Tamaulipas, off Barra del Tordo, 19 Aug 1979; 1 unsexed juvenile, sl 1.5 mm, 3 ov females, sl 4.1, 3.6, 5.1 mm, 1 female, sl 3.4, 4 males, sl 2.7, 2.6, 4.3, 5.4 mm, (ULLZ 239/USNM 1538562), Campeche, Isla Aguada, Laguna de Terminos, *Thalassia* beds, 05 Jan 1978; 1 male, sl 11.5 mm (ULLZ 88/USNM 1542715), Campeche, northeast of Champoton, grass beds, 07 Jan 1978; 1 female, sl 4.4 mm, 1 male, sl 4.1 mm (ULLZ 230/USNM 1542740), Campeche, 5 miles north of Seybaplaya, 06 Jan, 1977; 1 ov female, sl 3.9 mm, 1 male, sl 5.6 mm (ULLZ 93/USNM 1542718), Campeche, 5 miles north of Seybaplaya, intertidal rocks, corals, and sponges, 06 Jan 1977.

Panama. 1 male, sl 4.0 mm (ULLZ 13707/USNM 1547066), Bocas del Toro, grass beds and *Porites*, 2 m, 08 Aug 2011; 1 male, sl 3.7 mm (ULLZ 13708/USNM 1547067), Bocas del Toro, 08 Aug 2011, grass beds and *Porites*, 2 m.

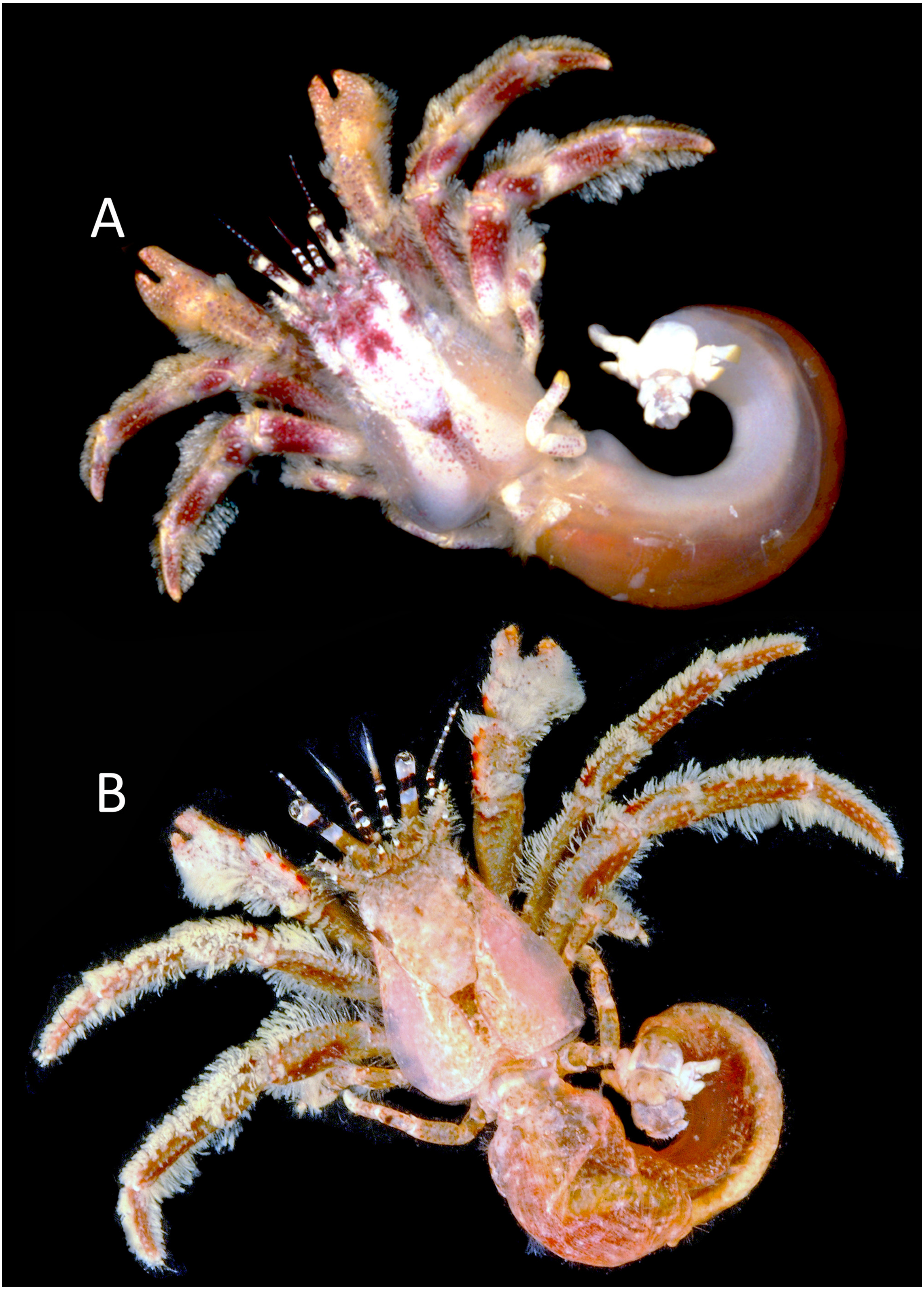

FIGURE 5. Color patterns of A, *Paguristes tortugae* s.s., male, sl 7.2 mm (ULLZ 4783/USNM 1540547), Florida Keys, Gulf of Mexico; B, *P. karenae* **n. sp.**, paratype male, sl 4.9 (ULLZ 8578/USNM 1543769), Gulf of Mexico. A, habitus, dorsal surface; B, habitus, dorsal surface.

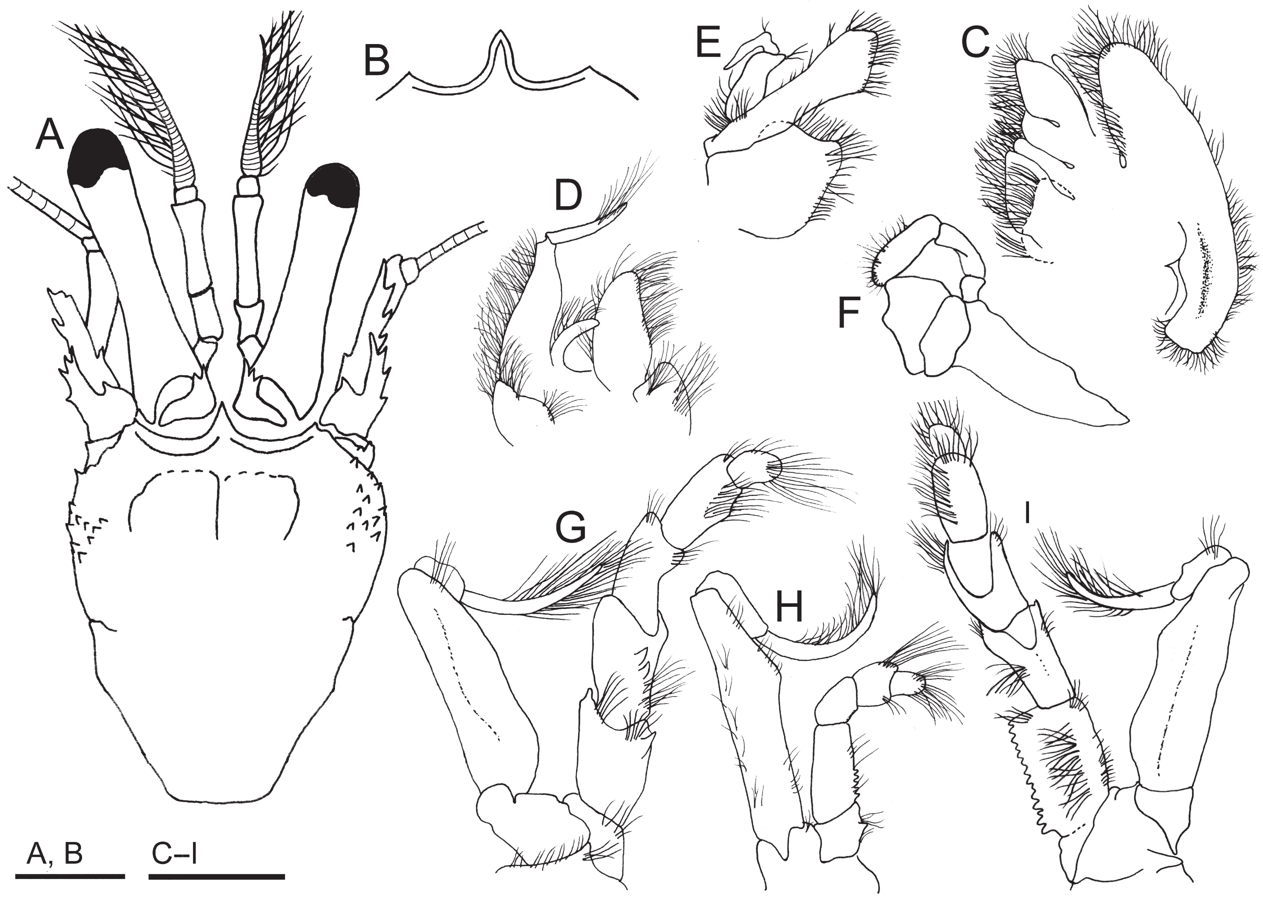

FIGURE 6. *Paguristes karenae* **n. sp.** A, C–I, paratype male, sl 4.9 mm (ULLZ 8578/USNM 1543769), Gulf of Mexico; B, *P. tortugae* s.s., female, sl 4.1 mm (ULLZ 11148/USNM 1545610), Belize, northwestern Caribbean. A, carapace shield and head appendages, dorsal surface, setae omitted; B, carapace shield anterior margin showing rostrum; C, right maxilla, internal surface; D, right first maxilliped, external surface; E, right maxillule, external surface; F, right mandible, internal surface; G, right third maxilliped, external surface; H, right second maxilliped, external surface; I, right third maxilliped, internal surface. Scale bars = 1.0 mm (A–I).

French Antilles. 1 male, sl 2.5 mm (UF 032561), Saint Martin, Caye Verte, reef with sand and seagrass, 1–3 m, 25 Apr 2012.

Diagnosis. Antennal flagellum slender with sparse setae 1–3 articles in length near joints of articles. Antennular peduncles not exceeding corneas, or exceeding corneas by less than 0.5 distal length of ultimate segment. Ocular peduncles subcylindrical, slightly narrower near midlength, always marked with distinct dark bands near midlength bordered by white distally and proximally, (often persisting in ethanol preserved specimens). Ocular acicles well separated by rostrum, with narrow anterior projection bifid or multifid, bearing a variable number of accessory spines laterally. Rostrum tapering evenly to an acute point. Cheliped manus dorsomesial margin bearing 3 strong, corneous-tipped spines. Cheliped carpus dorsomesial margins with 4 or 5 strong, corneous tipped, conical spines, color bright carmine red in life. Second pereopod carpus dorsal margin with row of acute spines and third pereopod carpus dorsal margin with 1 or more acute spines distally, bright carmine red in life. First maxilliped with epipod well developed. In life, carapace shield with patches of olive green to light brown, pereopods two and three with light brown to olive green background color, branchiostegites laterally translucent purple with some white spotting. Applicable GenBank sequence accession numbers from Craig & Felder (2021) are as follows for holotype, ULLZ 4782/USNM 1540546: (H3) MW160343; (12S) MW160976; (16S) MW167246.

Description. Thirteen pairs of biserial gills. Shield (Fig. 6A, B) sub-triangular, length approximately 1.4 times width. Dorsal surface central region convex; lateral surfaces bearing irregularly spaced small tubercles, spinules, and spines interspersed with sparse setae; anterior margins between rostrum and lateral projections distinctly concave, paralleled by well-defined marginal ridge; anterolateral angle obtuse and rounded bearing numerous irregularly spaced spines and spinules. Rostrum triangular, extending anteriorly beyond lateral projections, lateral margins sloping evenly to acute point and bearing fringe of setae. Lateral projections acute. Branchiostegite lateral surface with granular texture nearly obscured by tufts of long setae. Posterior carapace poorly calcified, lateral surfaces bearing scattered setae.

Ocular peduncles (Fig. 6A) subcylindrical, slightly narrower at midlength, diameter at base approximately equal to that of cornea, left longer than right; dorsomesial surface bearing tufts of long setae proximally. Ocular acicles (Fig. 6A) subtriangular, mesial borders unarmed and separated by rostrum; anterior projection bifid or multifid, lateral margin bearing 1 or more acute spines.

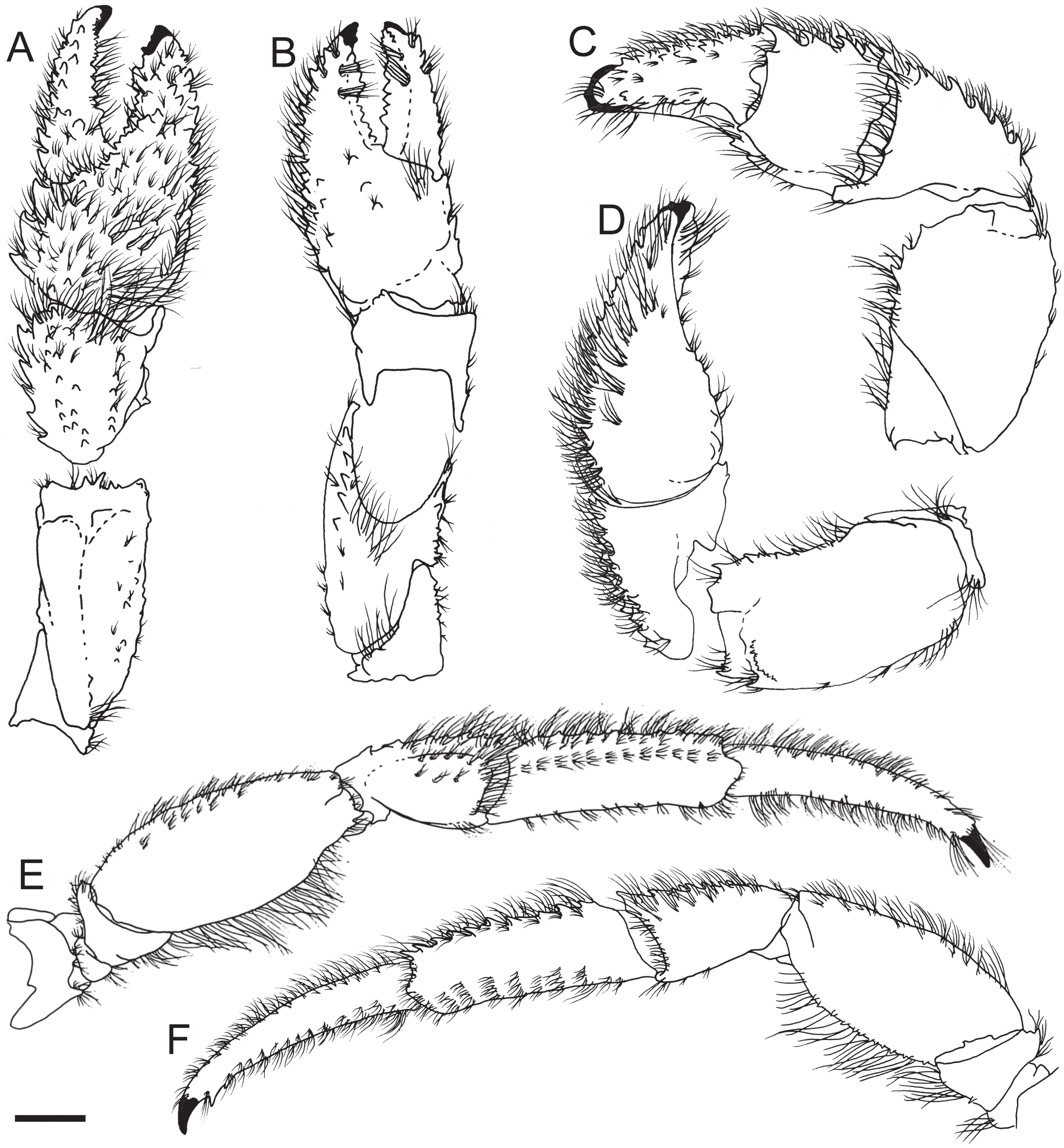

FIGURE 7. *Paguristes karenae* **n. sp.**, A–F, paratype, male, sl 4.9 mm (ULLZ 8578/USNM 1543769), Gulf of Mexico. A, right cheliped, dorsal surface; B, right cheliped, ventral surface; C, right cheliped, lateral surface; D, right cheliped, mesial surface; E, right second pereopod, lateral surface; F, right second pereopod, mesial surface. Scale bar = 1.0 mm (A–F).

Antennular peduncles (Fig. 6A) not extending anteriorly beyond cornea distal margin in holotype (exceeding cornea distal margin by approximately 0.5 length of ultimate segment in some paratypes); basal segment lateral surface bearing small spine.

Antennal peduncles (Fig. 6A) not extending anteriorly beyond cornea distal margin. Fifth segment without remarkable characteristics. Fourth segment dorsodistal angle bearing anteriorly angled spine. Third segment ventromesial distal angle bearing strong spine, somewhat obscured from dorsal view by dense fringe of setae. Second segment dorsolateral distal angle forming anterior projection terminating in single spine, lateral margin somewhat oblique, bearing 3 spines, dorsomesial distal angle bearing single spine. First segment dorsolateral distal angle bearing minute spine. Antennal acicles extending slightly beyond 0.5 mid-length of ocular peduncle, terminating in single spine; lateral margin bearing 2 or more spines (number variable among paratypes) interspersed with tufts of long setae; mesial border with 1 or more (number variable among paratypes) widely spaced spines partially obscured by dense fringe of setae. Antennal flagellum not extending beyond fingertips, sparse setae approximately 1–3 articles in length at joints of flagellar articles.

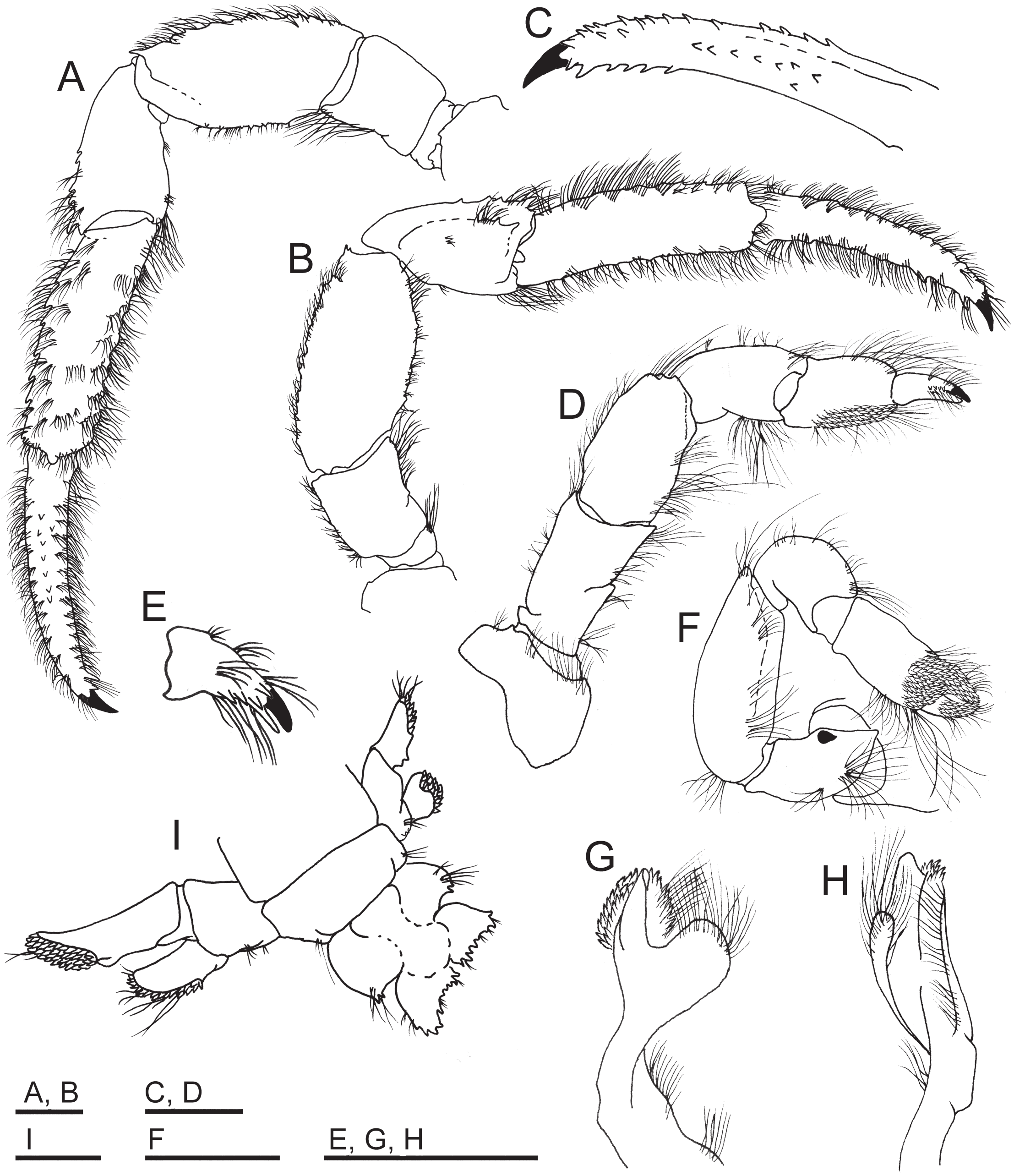

FIGURE 8. A–I, *Paguristes karenae* **n. sp.**, paratype, male, sl 4.9 mm (ULLZ 8578/USNM 1543769), Gulf of Mexico. A, right third pereopod, mesial surface; B, right third pereopod, lateral surface; C, right third pereopod dactyl, mesial surface, setae omitted; D, right fourth pereopod, lateral surface; E, fourth pereopod dactyl; F, right fifth pereopod, lateral surface; G, gonopod, mesial surface; H, gonopod, internal surface; I, telson and uropods, dorsal surface. Scale bars = 1.0 mm (A–I).

Mandible (Fig. 6F) with incisor edge calcareous; ultimate segment of palp broad, setose, length equal to combined length of penultimate and basal segments. Maxillule (Fig. 6E) proximal and distal endite mesial margins densely setose; endopod internal lobe distal angle bearing sparse tuft of bristles, external lobe recurved, length approximately 0.7 times that of internal lobe, terminal angle bearing sparse setae. Maxilla (Fig. 6C) proximal and distal endite mesial margins densely setose; endopod tapered distally, not overreaching distal apex of scaphognathite; scaphognathite recurved, margins densely setose. First maxilliped (Fig. 6D) proximal and distal endite mesial margins densely setose; endopod length approximately 0.7 times that of exopod; exopod tapering distally, lateral margin densely setose, flagellum elongate and densely setose; epipod well developed, margins densely setose. Second maxilliped (Fig. 6H) basis mesial margin bearing small blunt spine. Third maxilliped (Fig. 6G, I) endopod merus external surface bearing 2 or more strong, curved spines on mesial margin; ischium external surface distomesial angle bearing 1 spine; crista dentata well developed, lacking accessory tooth.

Chelipeds (Fig. 7A–D) subequal in size, similarly armed, opening transversely; dorsal surfaces of chelae and carpi densely covered with tufts of plumose setae partially obscuring armature beneath, longer setae forming dense fringe along dorsolateral and dorsomesial margins of chelae and carpus; both fixed and moveable finger with distal extremity terminating in hoof-like corneous claw. Dactyl length approximately 2.5 times maximum height; cutting edge bearing calcareous teeth decreasing in size distally and widely spaced tufts of stiff bristles; dorsal surface bearing irregularly spaced low tubercles and conical spines, many abutting tufts of setae or stiff bristles; dorsomesial surface bearing scattered low tubercles, each abutting tuft of setae; ventral surface cutting edge paralleled by longitudinal groove bearing widely spaced tufts of stiff bristles. Fixed finger not extending beyond moveable finger; cutting edge bearing numerous blunt calcareous teeth and scattered tufts of setae. Palm dorsal surface somewhat convex, bearing densely distributed conical tubercles and spines, some with corneous tips, most abutting tuft of setae (setae largely obscuring armature for most paratypes); dorsomesial margin well defined, bearing 3 conical spines with corneous tips; dorsolateral margin bearing row of numerous irregularly spaced conical spines, some with corneous tips; ventral and lateral surfaces bearing scattered low tubercles (blunt spines or conical tubercles in some larger paratypes) many abutting tufts of short setae. Carpus length approximately 0.5 times that of chela; dorsal surface midline bearing irregularly distributed conical spines interspersed tufts of setae; dorsomesial border well defined, armed with 4 (5 in some paratypes) conical spines with corneous tips, bright carmine red color in life; dorsolateral margin bearing continuous row of conical spines, some with corneous tips; dorsodistal margin with slight anterior projection near midline bearing small conical spines (number variable among paratypes) somewhat obscured by dense setae; lateral and mesial surfaces relatively smooth, setation sparse; ventrodistal angle forming hook-like projection bearing 1 or more small spines at distomesial extremity. Merus length approximately 2 times that of carpus, subtriangular in cross section; dorsal margin bearing irregularly spaced small spines proximally, transected subdistally by low ridge bearing conical spines, some with corneous tips; dorsodistal margin bearing conical spines near midline, some with corneous tips; mesial surface relatively smooth; ventromesial margin bearing row of conical spines distally; ventrolateral margin surface bearing row of irregularly spaced spines interspersed with long setae. Ischium mesial surface subtriangular; ventromesial margin bearing minute spines or spinules; ventrodistal margin bearing sparse tufts of setae. Coxa distal margin bearing dense fringe of setae; ventral surface densely setose.

Second pereopod (Fig. 7E, F) extending beyond cheliped by approximate length of second pereopod dactyl when both fully extended, terminating in single corneous claw, segments somewhat laterally compressed; dorsal margins of dactyl, propodus, carpus, and merus bearing dense fringes of setae obscuring underlying armature for many paratypes; ventral margins likewise. Dactyl length approximately 5.5 times maximum height, curved ventrally from lateral view, terminating in curved corneous claw with enlarged spine and tuft of stiff bristles proximally; dorsal and ventral margins each bearing row of corneous-tipped spines (minute in smaller paratypes), increasing somewhat in size distally, observable at high magnification from mesial view; mesial surface bearing scattered small corneous spines (more prominent and often broadly distributed in larger paratypes). Propodus length approximately 0.7–1.0 times that of dactyl (ratio slightly variable in paratypes); dorsal margin bearing row of spines somewhat obscured by dense fringe of setae (in mesial view); mesial and lateral surfaces armed with series of low transverse ridges each bearing small spinules (visible in holotype and larger paratypes); and abutting row of setae. Carpus length approximately 0.7 times that of propodus; dorsal margin armed with numerous (number varies among paratypes) conical spines with corneous tips, color deep carmine red in life; dorsolateral surface with pronounced longitudinal ridge bearing dense tufts of long setae; dorsomesial surface bearing tufts of setae arranged in transverse rows. Merus length approximately 2 times that of carpus; dorsal margin bearing dense fringe of setae arranged in a series of transverse rows; ventral margin bearing row of widely spaced conical spines (in mesial view); ventrolateral surface bearing scattered tufts of short setae; distolateral margin bearing conical spines distally (number and prominence varies among paratypes). Ischium mesial and lateral surfaces subtriangular. Coxa without distinguishing characters.

Third pereopod (Fig. 8A, B) not extending beyond claw of second pereopod, similar in proportion and armature to second pereopod except as noted here. Dactyl mesial surface bearing numerous corneous spines, more prominent and broadly distributed than those of second pereopod. Propodus mesial surface more tubercular and setose than that of second pereopod for most paratypes. Carpus dorsal margin with conical, corneous tipped spines restricted to distal 0.5; dorsodistal angle bearing somewhat enlarged conical spine. Merus lateral surface slightly convex; dorsolateral surface bearing series of transverse rugae; mesial surface bearing elongate oblique rugae. Ischium length approximately 0.5 times that of merus; mesial and lateral surfaces subrectangular. Sternite of third pereopod subrectangular, left and right each bearing rounded tubercle with dense tuft of setae.

Fourth pereopod (Fig. 8D) laterally compressed, not extending beyond distal margin of third pereopod merus. Dactyl (Fig. 8E) robust, terminating in curved corneous claw dense tuft of setae dorsally; dorsal margin bearing tufts of stiff bristles; ventrolateral surface bearing 1–3 stout teeth interspersed with bristles, most distal tooth somewhat enlarged and abutting base of preungal process. Preungal process well-developed, length slightly less than that of corneous claw. Propodus length approximately 2 times that of dactyl; dorsal margin bearing long setae distally; ventrolateral surface bearing oblong rasp extending approximately 0.7 distal length of segment. Carpus, merus, and ischium similar in length, dorsal and ventral margins of each bearing dense fringe of setae.

Fifth pereopod (Fig. 8F) chelate, with length of fixed finger subequal to that of dactyl; segments generally subcylindrical. Propodal rasp continuous across dactyl, fixed finger, and approximately 0.3 distal length of segment; ventromesial surface bearing dense patch of setae. Carpus somewhat recurved; dorsal margin bearing sparse setae. Merus lateral surface bearing irregular longitudinal row of setae near midline. Coxa lateral surface bearing dense tuft of setae and male sexual pore proximally.

Abdomen curled, poorly sclerotized. Male first (Fig. 8G, H) and second pleopods paired and modified as gonopods, pleopods 3–5 unpaired; first pleopod inferior lamella (Fig. 8G) lateral margin bearing fringe of setae, distal margin with numerous irregular rows of curved teeth extending onto external surface, internal lamella distal margin bearing fringe of long setae, external lamella extending slightly beyond inferior lamella of distal margin; basal segment of second pleopod bearing sparse tuft of long setae at superior mesial angle. Female first pleopods paired, pleopods 2–5 unpaired, pleopod 5 uniramous; paired gonopores on coxa of third pereopod; brood pouch large, subovate to subquadrate; eggs approximately 0.5–0.7 mm in diameter.

Uropods (Fig. 8I) strongly asymmetrical, left robust and elongate. Telson (Fig. 8I) weakly asymmetrical, left lobe somewhat larger than right, deep lateral incisions dividing anterior and posterior portions; anterior lobes subovate to subtriangular, distolateral angles each bearing 1 or more (number variable in paratypes) conical spines; posterior lobes subtriangular, left and right separated by well defined cleft, terminal margins each bearing scattered bristles and numerous conical spines, some with corneous tips (number, prominence, and precise orientation of spines variable in paratypes).

Size. Largest examined, male, sl 11.5 mm.

Color. Carapace shield with patches of olive green to light brown, pereopods two and three with light brown to olive green background color, branchiostegites laterally translucent purple with some white spotting, ocular peduncles with distinct dark brown to almost black bands near midlength (bands often persisting in preservation as dark pink to orange) bordered with white both proximally and distally (Fig. 5B). Spines on cheliped carpus dorsomesial margins bright carmine red with corneous tips. Spines on third pereopod carpus dorsal margin bright carmine red.

Etymology. The species name, "karenae", honors our colleague and friend, Karen Barkel (formerly Strasser), for reknown contributions to studies of decapod crustaceans, collections that assisted our efforts, and persistent urging that this new species be formally described.

Distribution and habitat. Broadly distributed across the Gulf of Mexico, eastern coast of South America, southeastern and southwestern Caribbean, and along the eastern coast of Florida; bathymetric distribution ranging between the intertidal zone and approximately 30 m in depth. Collected in arange of habitats including hard-bottom substrates, rubble, sandy bottoms with seagrass (*Thalassia*), reef communities, sponges, and coral (*Porites*).

Morphological variations. *Paguristes karenae* **n. sp.** shows a moderate range of intraspecific variation related to specimen size. Zones of spination are characteristic of the species, but within those zones, larger specimens exhibit fewer, more robust spines, especially on the ambulatory appendages. There are exceptions, however, as in the case of the third pereopod dactyl mesial surface, where larger individuals show a broad distribution of corneous spines with moderate prominence, compared to the scattering of minute spines seen in most smaller individuals. In addition to variability of spination related to size, eyestalk shape shows some variance, with the eyestalks of smaller specimens tending to have a broader proximal base relative to the cornea, accompanied by a greater taper at midlength when compared to the eyestalks of larger individuals.

Two notable morphological variations seemingly unrelated to size can be found among paratypes. In both large and small individuals, the cheliped carpus dorsomesial margin is typically armed with four prominent red spines, but for some paratypes there is a moderately sized fifth accessory spine at the base of the fourth most distal spine. In addition, antennular peduncle length relative to that of the eyestalk varies, with the antennular peduncle exceeding the cornea distal margin for some paratypes.

Remarks. Although the occurrence of *P. tortugae* in the northern Gulf of Mexico was once considered tentative (McLaughlin & Provenzano 1974), numerous records based on ULLZ collection data confirm its occurrence throughout the Gulf of Mexico and Caribbean over a range of depths (Table 1), as suggested previously by Felder *et al.* (2009: footnote 200, 1096). Collection data for *P. karenae* **n. sp.** specimens available to us indicate that the geographic and bathymetric distributions of *P. karenae* **n. sp.** approximate those of *P. tortugae*. This is evident even at very local scales, with examples of *P. tortugae* and *P. karenae* **n. sp.** specimens housed at USNM (including many recently accessioned from ULLZ) collected from overlapping localities and similar habitats. Despite this sympatry, consistent differences in color between the two species, along with corresponding morphological characters, provide support for their separation, and molecular phylogenetic analysis confirms the two as distinct sister lineages (Craig & Felder 2021).

McLaughlin & Provenzano (1974) cited color and pattern as diagnostic of at least five of the original constituent species of the *P*. *tortugae* complex. Historically, accounts detailing the color of *P*. *tortugae* itself established two color forms, both of which possess eyestalks bearing dark bands bordered by white near midlength (Wass 1955; Holthuis 1959; Provenzano 1959, 1965; Williams 1965; McLaughlin & Provenzano 1974; Strasser & Price 1999). Photographic evidence compiled by us in the course of long-term decapod biodiversity surveys in the western Atlantic corroborates literary accounts of these two sympatric color forms, both of which are morphologically consistent with existing diagnosis of *P*. *tortugae sensu* McLaughlin & Provenzano (1974). In our photographic accounts, specimens with a whitish to light purple background color (Fig. 5A) are considered herein to correspond to Schmitt's (1933) *P*. *tortugae*, a form earlier documented as having a relatively light coloration (Provenzano 1959; Williams 1965; McLaughlin & Provenzano 1974) with rosy to somewhat purple walking legs (Holthuis 1959; Provenzano 1965). The second color form, described in the present work as *P. karenae* **n. sp.** (Fig. 5B), has an overall light brown to olive green carapace, as well as distinctly red spines on the carpi of the walking legs, particularly the mesial margin of the manus and carpus of the cheliped. This coloration had been previously observed by other authors (Provenzano 1959; Holthuis 1959; Williams 1965), and is considered herein to correspond to the "darker" forms of McLaughlin & Provenzano (1974).

Despite their overall similarity to one another, morphological differentiation of *Paguristes tortugae* and *P. karenae* **n. sp.** can be made by considering the precise shape of the rostrum. For both species, the rostrum is well developed, extending past the lateral projections of the shield and separating the ocular acicles. However, in *P. karenae* **n. sp.** the rostrum tapers evenly to an acute point (Fig. 6A), whereas that of *P. tortugae* exhibits slightly rounded shoulders to either side of the rostrum apex (Fig. 6B). Inclusion of USNM 151492 in our synonymy of *P*. *karenae* is based on this criterion, with Williams (1984: fig 144) showing clearly a triangular and evenly tapered rostrum. In addition to its distinct rostral taper, oblique rugae are present on the merus of the second pereopod in our new species, and these are lacking in *P*. *tortugae*.

Recognition of *P*. *karenae* **n**. **sp**. casts uncertainty on identifications of *P*. *tortugae* made by previous authors. In most cases, no evidence is provided that we can use to definitively distinguish between *P*. *karenae* **n**. **sp**. and *P*. *tortugae* s.s. In previous studies, Provenzano (1959) and McLaughlin & Provenzano (1974) are often given as the primary references for determining the identification of *P*. *tortugae* specimens. While both of these works note variability in coloration of *P*. *tortugae* sensu lato (s.l.), the color of subsequently reported specimens is rarely given further mention. Numerous checklists, observational accounts, ecological studies, and taxonomic keys do not address details of coloration or morphology among the specimens they designate as *P*. *tortugae* s.l. (Schmitt 1935; Wass 1955; Provenzano 1961; Soto 1980; Abele & Kim 1986; Holmquist 1989; Martinez-Iglesias & Gomez 1989; Mantelatto & Sousa 2000; Majon-Cabezas *et al.* 2002; Mantelatto & Garcia 2002a, 2002b, 2002c; Raz-Guzman *et* *al.* 2004; Rahayu 2005; Tagliafico *et al.* 2005; Barros-Alves *et al.* 2015; Lemaitre & Tavares 2015; Lima & Santana 2017; Poupin 2018). Thus, our herein reported synonymies applicable to *P. karenae* **n. sp.** is limited.

Discussion

Composition of the *Paguristes tortugae* complex originally included seven species, *Paguristes tortugae*, *P. hewatti* (= *Areopaguristes hewatti*), *P. hernancortezi*, *P. angustithecus*, *P. perplexus*, *P. anomalus*, and *P. invisisacculus* (= *Pseudopaguristes invisisacculus*), all exhibiting a dense fringe of setae on the thoracic appendages. Subsequently, the complex grew to include newly discovered species. Campos & Sanchez (1995) included two from northern Colombia, *Paguristes zebra* and *P. werdingi.* More recent additions from the western Atlantic are *P. maclaughlinae* Martinez-Iglesias & Gomez, 1989 of Cuba, and the Brazilian species, *P. scarabinoi* Lima & Santana, 2017. Genetic data are not yet available to confirm the phylogenetic affinities of these additional species to the *P. tortugae* complex, though such analyses have added *A. tudgei* to the complex (Craig & Felder 2021).

Areopaguristes rafaeli **n. sp.** and its sister species *A. hummi* could be considered members of the *Paguristes tortugae* complex based on possession of a dense fringe of setae on the thoracic appendages, the currently used broad diagnostic criteria for the complex. However, genetic evidence does not support a close affinity between *A. hummi* sensu stricto (s.s.) or *A. rafaeli* **n. sp.** and *P. tortugae* itself. Instead, *A. hummi* and *A. rafaeli* **n. sp.** were shown to be distant relatives of *P. tortugae* in our molecular phylogenetic analyses (Craig & Felder 2021) of western Atlantic members of *Paguristes*, *Areopaguristes*, and *Pseudopaguristes.* This is consistent with the morphological disparities evident when *A. hummi* and *A. rafaeli* **n. sp.** are compared to other species of the *Paguristes tortugae* complex, including comparisons with *A. hewatti,* which is morphologically and genetically most similar to *P. tortugae* (Table 2).

Besides the characteristic fringe-like distribution of setae on the thoracic appendages, unifying morphological characters for the *Paguristes tortugae* complex, as historically used, have remained elusive (Provenzano & Rice 1966; McLaughlin & Provenzano 1974). Some characters that are confirmed as diagnostic at the species level, such as the form of the brood pouch and the coloration of the cephalic appendages (McLaughlin & Provenzano 1974; Provenzano 1959, 1965), may also prove useful in delimiting subgroups within the complex when combined with genetic findings. Aside from *Areopaguristes tudgei* Lemaitre & Felder, 2012 and *P. anomalus*, two genetic allies of *P. tortugae* that lack brood pouches entirely, other presumed or genetically confirmed associates of *P. tortugae* can be grouped into three divisions based on brood pouch morphology: those with subovate to subquadrate pouches (*P. tortugae*, *A. hewatti*, *P. zebra*, *P. hernancortezi*), those with slender, blade shaped pouches (*P. angustithecus*, *P. scarabinoi*), and those with triangular pouches (*P. perplexus*, *Pseudopaguristes invisisacculus*). Findings of genetic phylogenetic analyses have so far mirrored some of these groupings by recovering a well-supported clade including *Paguristes tortugae*, *A. hewatti*, and *P. hernancortezi*, all species having subovate to subquadrate brood pouches. Species possessing blade-shaped brood pouches are found only outside of that genetic clade (Craig & Felder 2021). Additionally, coloration and patterning of the head appendages is somewhat predictive of these brood pouch group assignments, with subovate to subquadrate brood pouches correlated with banded or spotted eyestalks. These two trends can be extended and applied to species for which genetic data is not yet available such as *P. zebra*, a species with irregularly banded eyestalks and a subovate brood pouch that shares many additional morphological characters with genetically confirmed *P. tortugae* complex constituents (Table 2).

Some species typically considered as constituents of the *P. tortugae* complex are not accommodated by phylogenetically supported trends regarding brood pouch shape or head appendage coloration. *Paguristes angustithecus* has banded eyestalks, a feature that has historically prompted the proposal of an alliance with *P. tortugae* and *A. hewatti* (McLaughlin & Provenzano 1974). However, the banded eyestalks of *P. angustithecus* are not accompanied by a subovate or subquadrate brood pouch. Segregation of *P. angustithecus* from the patterned eyestalk clade is further prompted when the length of the setae on the antennal flagellum is compared among these potentially allied species (Table 2). The long setae of the antennal flagellum, along with a blade-shaped brood pouch, distinguish *P. angustithecus* from *P. tortugae* and its closest allies, but unite it with *P. scarabinoi.* When *P. angustithecus* is not considered a constituent of the patterned eyestalk clade, the species remaining are exemplified by *P. tortugae*, sharing many potentially diagnostic characters. This raises suspicion that *P. scarabinoi* and *P. angustithecus* together could represent a unified phylogenetic subgroup independent of *P. tortugae* and its closest allies, rather than being anomalies among them.

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