

**Revision of *Pylopagurus* and *Tomopagurus* (Crustacea: Decapoda: Paguridae), with descriptions of new genera and species. Addendum and taxonomic summary**

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*Abstract.*—The discovery of two new species, *Enallopagurus provenzanoi*, and *Enallopaguropsis williamsi*, has required an addendum and concluding part to the revisionary study of the “*Pylopagurus-Tomopagurus*” group of genera. The diagnoses of *Enallopagurus* McLaughlin and *Enallopaguropsis* McLaughlin, are emended, and a corrected key to the genera is provided. The discovery of additional specimens of *Phimochirus randalli* (Provenzano) from the Gulf of Mexico has provided supplemental information on the morphology, color, and distribution of this uncommon species; it is rediagnosed and illustrated. Also provided is a summary of the original taxonomic assignments in part 1 (published in 1981) of this revisionary study, and the subsequent changes, corrections, deletions, and additions that have occurred since then. An updated list of the 13 genera, two subgenera, and 64 valid species currently recognized in the “*Pylopagurus-Tomopagurus*” group, is presented.

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McLaughlin (1981a) proposed the new genera *Enallopagurus* McLaughlin, 1981a and *Enallopaguropsis* McLaughlin, 1981a, for five relatively uncommon eastern Pacific hermit crab species that had been included by earlier authors in the genus *Pylopagurus* A. Milne-Edwards & Bouvier, 1891. To *Enallopagurus*, McLaughlin (1981a) assigned *Pylopagurus affinis* Faxon, 1893, *P. coronatus* (Benedict, 1892), and *P. spinicarpus* Glassell, 1938; *Enallopaguropsis* included *P. guatemoci* Glassell, 1937, and *Pylopagurus hancocki* Walton, 1954. One of the primary characters that McLaughlin (1981a) used to differentiate between *Enallopagurus* and *Enallopaguropsis* was the rows of scales on the propodal rasp of the fourth pereopod. In a subsequent, more detailed account of these two genera, McLaughlin (1982) placed *Enallopaguropsis hancocki* in synonymy with *E. guatemoci*

and added the new species *E. janetae* McLaughlin, 1982. In the present addendum and concluding part of the revision of the “*Pylopagurus-Tomopagurus*” group of genera, two new species, one each of *Enallopagurus*, and *Enallopaguropsis*, are described.

Recent sampling off the Louisiana coast in the northern Gulf of Mexico has yielded a number of additional specimens of *Phimochirus randalli* (Provenzano, 1961), a species discussed by McLaughlin (1981b) and at the time known only from the Bahamas Islands and Caribbean region. Examination of these Gulf of Mexico specimens revealed a number of morphological details that complement previous definitions of *P. randalli*. Furthermore, Provenzano's (1961:161) color description was incomplete as it was based on faded, preserved specimens, whereas for this study

live specimens from the Gulf of Mexico were available and photographed (D. L. Felder, pers. comm.). *Phimochirus randalli* is herein rediagnosed, and illustrated.

Since the publication of part 1 (McLaughlin 1981a) of the six-part revisionary study of the “*Pylopagurus-Tomopagurus*” group of genera, several new species have been added that have necessitated emendations of generic diagnoses, and two new genera have been erected. Some of the taxonomic assignments made in part 1 have been changed in light of new evidence gleaned from direct examination of type materials not initially available. In some cases, new morphological discoveries, such as the existence of short sexual tubes in some species of *Pylopagurus* sensu stricto (see McLaughlin & Lemaitre 2001), or the existence of short protrusions of the vas deferentia in the form of tubular papillae in *Agaricochirus* McLaughlin, 1981a, *Enallopagurus*, and *Enallopaguropsis* (see McLaughlin 2003, this study), have required adjustments to our concept of these genera. In the new species of the latter two genera herein described, the morphology of the terminal margin of the telson has been found to deviate from the original generic diagnoses. As this margin shape was used as a character in the updated generic key provided by McLaughlin & Lemaitre (2001:480), that key now requires corrections. Also, several taxa have been synonymized since part 1 was published, whereas *Pylopagurus liochele* Barnard, 1947, a taxon tentatively assigned in parts 1 and 2 (McLaughlin 1981a, 1981b) to *Phimochirus* McLaughlin, 1981a, was transferred by McLaughlin (1988) to *Pagurus* Fabricius, 1775, a genus not considered part of the “*Pylopagurus-Tomopagurus*” group. McLaughlin’s (1981a) genus *Australeremus* was reduced by de Saint Laurent & McLaughlin (2000) to a subgenus of *Lophopagurus* McLaughlin, 1981a. Thus, it was felt useful to have in a single convenient publication, a summary of the taxonomic assignments, changes, corrections, and additions that have occurred during the 21+

years that have elapsed since the appearance of part 1 of the revision of this group. There are currently 13 genera, two subgenera, and 64 valid species known in this group (see Table 1).

Materials used in this study are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), and University of Louisiana at Lafayette (ULLZ). The specimens of the new species of *Enallopagurus* and *Enallopaguropsis* were collected by Dr. Anthony J. Provenzano, Jr. aboard the R/V *John Elliott Pillsbury*, of the Rosenstiel School of Marine and Atmospheric Science, University of Miami, Florida. The new material of *Phimochirus randalli* was collected by Dr. Darryl L. Felder aboard the R/V *Pelican*, of the Louisiana Universities Marine Consortium, Cocodrie. The interpretation of the ocular acicle is used in accordance with Forest et al. (2000), rather than that of Boyko & Harvey (1999). A single measurement, 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. Other abbreviations used are: ovig, ovigerous female; sta, station.

#### *Enallopagurus* McLaughlin, 1981a

*Pylopagurus*: Walton, 1954:140 (in part).—Scanland & Hopkins, 1969:257 (in part) [Not *Pylopagurus* A. Milne-Edwards & Bouvier, 1891].

*Enallopagurus* McLaughlin, 1981a:7; 1982:843; 2003:122.

*Emended diagnosis*.—Eleven pairs of biserial gills. Ocular acicle triangular or subovate, usually with strong submarginal spine. Sternite of third maxillipeds with spine on either side of midline. Third maxillipeds each with well-developed crista dentata, 1 accessory tooth; merus with or without dorsodistal spine. Maxillule with internal lobe moderately well produced, with 1 terminal bristle; external lobe weakly produced.

Table 1.—List of valid names of “*Pylopagurus-Tomopagurus*” group of taxa.

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<i>Pylopagurus</i> A. Milne-Edwards & Bouvier, 1891 sensu stricto	
<i>P. discoidalis</i> (A. Milne-Edwards, 1880)	
<i>P. holmesi</i> Schmitt, 1921	
<i>P. pattiae</i> Lemaitre & Campos, 1993	
<i>P. macgeorgei</i> McLaughlin & Lemaitre, 2001	
<i>P. gorei</i> McLaughlin & Lemaitre, 2001	
<i>Lophopagurus</i> ( <i>Lophopagurus</i> ) McLaughlin, 1981a	
<i>L. (L.) foresti</i> McLaughlin & Gunn, 1992	
<i>L. (L.) lacertosus</i> (Henderson, 1888)	
<i>L. (L.) nanus</i> (Henderson, 1888)	
<i>L. (L.) nodulosus</i> McLaughlin & Gunn, 1992	
<i>L. (L.) pumilus</i> de Saint Laurent & McLaughlin (2000)	
<i>L. (L.) thompsoni</i> (Filhol, 1885)	
<i>Lophopagurus</i> ( <i>Australeremus</i> ) McLaughlin, 1981a	
<i>L. (A.) cookii</i> (Filhol, 1883)	
<i>L. (A.) eltaninae</i> McLaughlin & Gunn, 1992	
<i>L. (A.) cristatus</i> (H. Milne Edwards, 1836)	
<i>L. (A.) kirkii</i> (Filhol, 1883)	
<i>L. (A.) laurentae</i> (McLaughlin & Gunn, 1992)	
<i>L. (A.) stewarti</i> (Filhol, 1883)	
<i>L. (A.) triserratus</i> (Ortmann, 1892)	
<i>Rhodochirus</i> McLaughlin, 1981a	
<i>R. rosaceus</i> (A. Milne-Edwards & Bouvier, 1893)	
<i>R. hirtimanus</i> (Faxon, 1893)	
<i>Phimochirus</i> McLaughlin, 1981a	
<i>P. operculatus</i> (Stimpson, 1859)	
<i>P. californiensis</i> (Benedict, 1892)	
<i>P. venustus</i> (Bouvier, 1898)	
<i>P. roseus</i> (Benedict, 1892)	
<i>P. randalli</i> (Provenzano, 1961)	
<i>P. holthuisi</i> (Provenzano, 1961)	
<i>P. occlusus</i> (Henderson, 1888)	
<i>P. leurocarpus</i> McLaughlin, 1981b	
<i>Haigia</i> McLaughlin, 1981a	
<i>H. diegensis</i> (Scanland & Hopkins, 1969)	
<i>Agaricochirus</i> McLaughlin, 1981a	
<i>A. boletifer</i> (A. Milne-Edwards & Bouvier, 1893)	
<i>A. alexandri</i> (A. Milne-Edwards & Bouvier, 1893)	
<i>A. cavimanus</i> (Chace, 1939)	
<i>A. erosus</i> (A. Milne-Edwards, 1880)	
<i>A. gibbosimanus</i> (A. Milne-Edwards, 1880)	
<i>A. hispidus</i> (Benedict, 1892)	
<i>A. echinatus</i> McLaughlin, 1982	
<i>A. acanthinus</i> McLaughlin, 1982	
<i>Anisopagurus</i> McLaughlin, 1981a	
<i>A. bartletti</i> (A. Milne-Edwards, 1880)	
<i>A. pygmaeus</i> (Bouvier, 1918)	
<i>A. vossi</i> Lemaitre & McLaughlin, 1996	
<i>A. actinophorus</i> Lemaitre & McLaughlin, 1996	
<i>A. hopkinsi</i> Lemaitre & McLaughlin, 1996	

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Table 1.—Continued.

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	<i>Manucomplanus</i> McLaughlin, 1981a
<i>M. cervicornis</i> (Benedict, 1892)	
<i>M. spinulosus</i> (Holthuis, 1959)	
<i>M. longimanus</i> (Faxon, 1893)	
<i>M. varians</i> (Benedict, 1892)	
<i>M. ungulatus</i> (Studer, 1883)	
	<i>Enallopagurus</i> McLaughlin, 1981a
<i>E. spinicarpus</i> (Glassell, 1938)	
<i>E. affinis</i> (Faxon, 1893)	
<i>E. coronatus</i> (Benedict, 1892)	
<i>E. provenzanoi</i> , new species	
	<i>Enallopaguropsis</i> McLaughlin, 1981a
<i>E. guatemoci</i> (Glassell, 1937)	
<i>E. janetae</i> McLaughlin, 1982	
<i>E. williamsi</i> , new species	
	<i>Tomopagurus</i> A. Milne-Edwards & Bouvier, 1893
<i>T. rubropunctatus</i> A. Milne-Edwards & Bouvier, 1893	
<i>T. cokeri</i> (Hay, 1917)	
<i>T. macLaughlinae</i> Haig, 1976	
<i>T. cubensis</i> (Wass, 1963)	
<i>T. wassi</i> McLaughlin, 1981a	
<i>T. purpuratus</i> (Benedict, 1892)	
<i>T. merimaculosus</i> (Glassell, 1937)	
<i>T. chacei</i> (Wass, 1963)	
	<i>Protoniopagurus</i> Lemaitre & McLaughlin, 1996
<i>P. bioperculatus</i> Lemaitre & McLaughlin, 1996	
	<i>Pylopaguridium</i> McLaughlin & Lemaitre, 2001
<i>P. markhami</i> McLaughlin & Lemaitre, 2001	

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Right cheliped with subovate or subrectangular chela. Left cheliped with chela triangular in cross-section, but dorsal surface not elevated into prominent keel or crest. Dorsodistal spine of carpi of second and third pereopods lacking. Sternite of third pereopods with subcircular, subovate or subquadrate anterior lobe. Sternites of third to fifth pereopods often with capsulate setae. Fourth pereopod with propodal rasp consisting of single row of corneous scales; dactyl with small preungual process usually present.

Males with paired gonopores, no distinct sexual tubes but occasionally with vas deferens protruded to form short tubular papilla, usually on right; without paired pleopods, with 3 uniramous or weakly biramous left pleopods on somites 3–5. Fe-

males with paired gonopores, paired first pleopods modified as gonopods, 4 unpaired left pleopods, second to fourth with both rami well-developed, fifth usually uniramous.

Uropods symmetrical or asymmetrical. Telson without indication of division into anterior and posterior portions; terminal margin entire or with inconspicuous median indentation, unarmed.

*Remarks.*—Faxon (1893, 1895: pl. 12, fig. 2e) reported that his single male specimen of *Pylopagurus affinis* (= *Enallopagurus affinis*) had the vas deferentia extruded as “small threads” from both gonopores. McLaughlin (1982) reexamined Faxon’s (1893) specimen and concluded that while there were slight protrusions, these were more probably an artifact of preservation

rather than actual, very small sexual tubes. Since McLaughlin's (1982) study, our information on and understanding of sexual tubes in the Paguridae has increased substantially. Among the "*Pylopagurus-Tomopagurus*" group, species of *Enallopaguropsis* and *Agaricochirus* can also have the vas deferentia protruded as tubular papillae, albeit not as a distinct sexual tube. In other Paguridae, similar protrusions are known to occur in genera such as *Discorsopagurus* McLaughlin, 1974, *Paguritta* Melin, 1939, and *Pagurus* (see de Saint Laurent 1970, McLaughlin & Lemaitre 1993, McLaughlin 2003). However, as reported by McLaughlin & Lemaitre (2001), short but distinct sexual tubes are present in some species of *Pylopagurus* sensu stricto. Recently, McLaughlin & Jensen (1996) found a very small sexual tube developed on the right coxa of males of *Parapagurodes hartae* McLaughlin & Jensen, 1996, and Komai (1998) provisionally transferred two Japanese species formerly assigned to *Pagurus* (*P. gracilipes* Stimpson, 1858 and *P. nipponensis* Yokoya, 1933), to *Parapagurodes* McLaughlin & Haig, 1973, because of the observed small sexual tubes in males of both species.

McLaughlin (1981a, 1982) included Faxon's (1893) *Pylopagurus affinis* in *Enallopagurus*, despite the fact that Faxon described the propodal rasp of the fourth pereopod as "multiserial". The type specimen has been reexamined, and Faxon's description and subsequent illustration (Faxon 1895: pl 12, fig. 2d) found to be in error; the propodal rasp of the fourth pereopod actually has a single row of scales. This species is retained in *Enallopagurus*, although this generic assignment is still provisional given that *E. affinis* is known only from the male holotype.

Until the discovery of the new species of *Enallopagurus* described herein, the genus had been considered exclusively an eastern Pacific taxon. Although the right cheliped of this new species lacks the operculate-like conformation seen in the other three species

assigned to the genus, the unarmed carpi of the second and third pereopods, the single row of scales on the propodal rasp of the fourth pereopod, and the presence in females of paired first gonopods, support its placement in the genus. The terminal margin of the telson in this new species of *Enallopagurus* has a minute median indentation and is not clearly entire as described in the original generic diagnosis (McLaughlin 1981a, 1982); thus, the need for the emendation. An updated key to the species of *Enallopagurus* is provided following the description of this new species.

***Enallopagurus provenzanoi*, new species**  
Figs. 1, 2

*Holotype*.—Ovig. ♀ (sl = 2.40 mm), R/V John Elliott Pillsbury, sta 581, 21°05'N, 86°23'W, Arrowsmith Bank, 146–265 m, 22 May 1967, USNM 1007525.

*Paratype*.—1 ♂ in poor condition (sl = 1.80 mm), same data as holotype, USNM 1007526.

*Description*.—Shield (Fig. 1a) longer than broad; anterior margin between rostrum and lateral projections slightly concave; anterolateral margins sloping; posterior margin truncate, dorsal surface glabrous. Rostrum triangular, terminating acutely. Lateral projections rounded, unarmed.

Ocular peduncle approximately 0.65 length of shield, moderately stout, with cornea slightly dilated; ocular acicles subtriangular, each terminating subacutely, with moderately well-developed submarginal spine (not always visible in dorsal view); separated basally by approximately basal width of 1 acicle.

Antennular peduncle overreaching ocular peduncle by 0.35–0.50 length of ultimate segment; ultimate and penultimate segments unarmed; basal segment with small spine on lateral face.

Antennal peduncle slightly shorter to equaling length of ocular peduncle. Fifth and fourth segments with scattered short se-

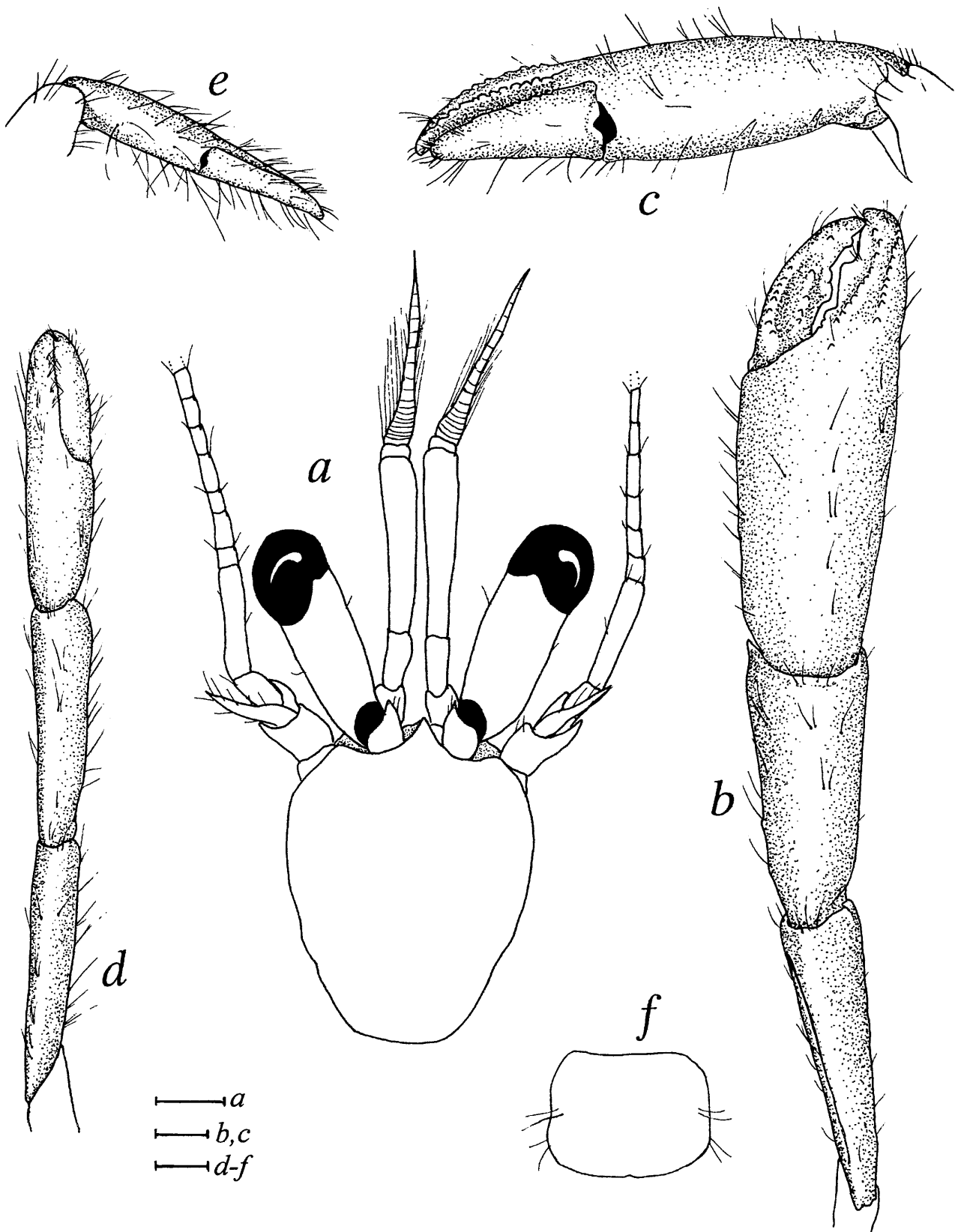


Fig. 1.—*Enallopagurus provenzanoi*, new species, holotype ovig ♀ (sl = 2.40 mm), northwestern Caribbean, R/V *John Elliott Pillsbury*, sta 581, USNM 1007525. a, shield and cephalic appendages, dorsal; b, right cheliped, dorsal; c, chela of same, mesial; d, left cheliped, dorsal; e, chela of same, mesial; f, telson, dorsal. Scales equal 0.50 mm (a), 1.00 mm (b, c), and 0.5 mm (d–f).

tae. Third segment with acute spine at ventrodistal angle. Second segment with dorsolateral distal angle produced, terminating in small spine; dorsomesial distal angle with small spine. First segment produced ventrally and with acute spine on ventrolateral margin. Antennal acicle moderately short, reaching only to distal margin of fourth peduncular segment. Flagellum long, with 1 or 2 short setae every several articles.

Sternite of third maxillipeds with strong spine on either side of midline.

Right cheliped (Figs. 1b, c) elongate, slender, overreaching left by length of dactyl. Dactyl approximately 0.75 length of palm, with row of small spines on proximal half of dorsomesial margin, separated from similar short row near cutting edge by shallow sulcus; cutting edge with 1 prominent double tooth in proximal half and single prominent tooth in distal half; mesial and ventral surfaces with few short setae. Palm exceeding carpus by approximately 0.20 own length; dorsal surface convex, unarmed, but with sparse tufts of setae, dorsomesial and dorsolateral margins not delimited; mesial, lateral and ventral surfaces also with sparse tufts of setae; fixed finger with row of low spines on dorsolateral margin and second row adjacent to cutting edge; latter with 2 or 3 small and 1 large broad calcareous teeth. Carpus slightly shorter than merus, subtriangular; dorsomesial and dorsolateral margins not delimited, surfaces unarmed but with scattered setae, 1 prominent spine on distomesial margin. Merus triangular, margins and surfaces unarmed, but with scattered short setae. Ischium unarmed.

Left cheliped (Figs. 1d, e) with dactyl approximately as long as palm; surfaces of dactyl, fixed finger and palm all unarmed but with sparse tufts of setae. Carpus only slightly shorter than merus; surfaces of both segments and ischium unarmed but with scattered short to moderately long setae.

Second and third pereopods (Figs. 2a, b) long and slender. Dactyls longer than pro-

podi; dorsal surfaces with few short setae; ventral margins each with row of 10–12 corneous spines and few short setae. Propodi approximately twice as long as carpi; dorsal surfaces with few setae; ventral margins each with 3 or 4 corneous spines, longest on third pereopod. Carpi less than half length of meri, unarmed, but with scattered setae dorsally and ventrally. Meri and ischia unarmed, but with dorsal and ventral sparse tufts of setae.

Fourth pereopod (Fig. 2d) with small preungual process on dactyl.

Sternite of third pereopods with reduced, slender anterior lobe. Sternites of fourth and fifth pereopods with capsulate setae (Fig. 2c). Telson (Fig. 1f) without indications of division into anterior and posterior portions; terminal margin broadly rounded, with inconspicuous median indentation, unarmed.

*Color.*—Overall body and appendage color very pale yellow. Ocular peduncles with white and yellow chromatophores and dark red longitudinal stripe on ventromesial and ventrolateral surfaces forming an elongate U-shaped pattern; corneas black with “frosted” overtone. Chelipeds each with few scattered orange spots. Dactyls of second and third pereopods with 2 extremely faint yellow bands, most apparent on second. (From A. J. Provenzano, Jr., field notes).

*Affinities.*—This species, known from only two specimens, bears certain habitat and morphological similarities to *Pylopagurus pattiae* Lemaitre & Campos, 1993. Both have been found living in membranous tubes and both have similarly elongate and weakly armed chelipeds. However, in addition to differences in generic characters, *E. provenzanoi* is easily distinguished from *P. pattiae* by the armature of the dactyl and fixed finger of the right chela, greater number of spines on the ventral margins of the dactyls of the second and third pereopods, unarmed ambulatory carpi, and structure of the telson.

*Habitat.*—The holotype was found living in a semi-transparent polychaete tube.

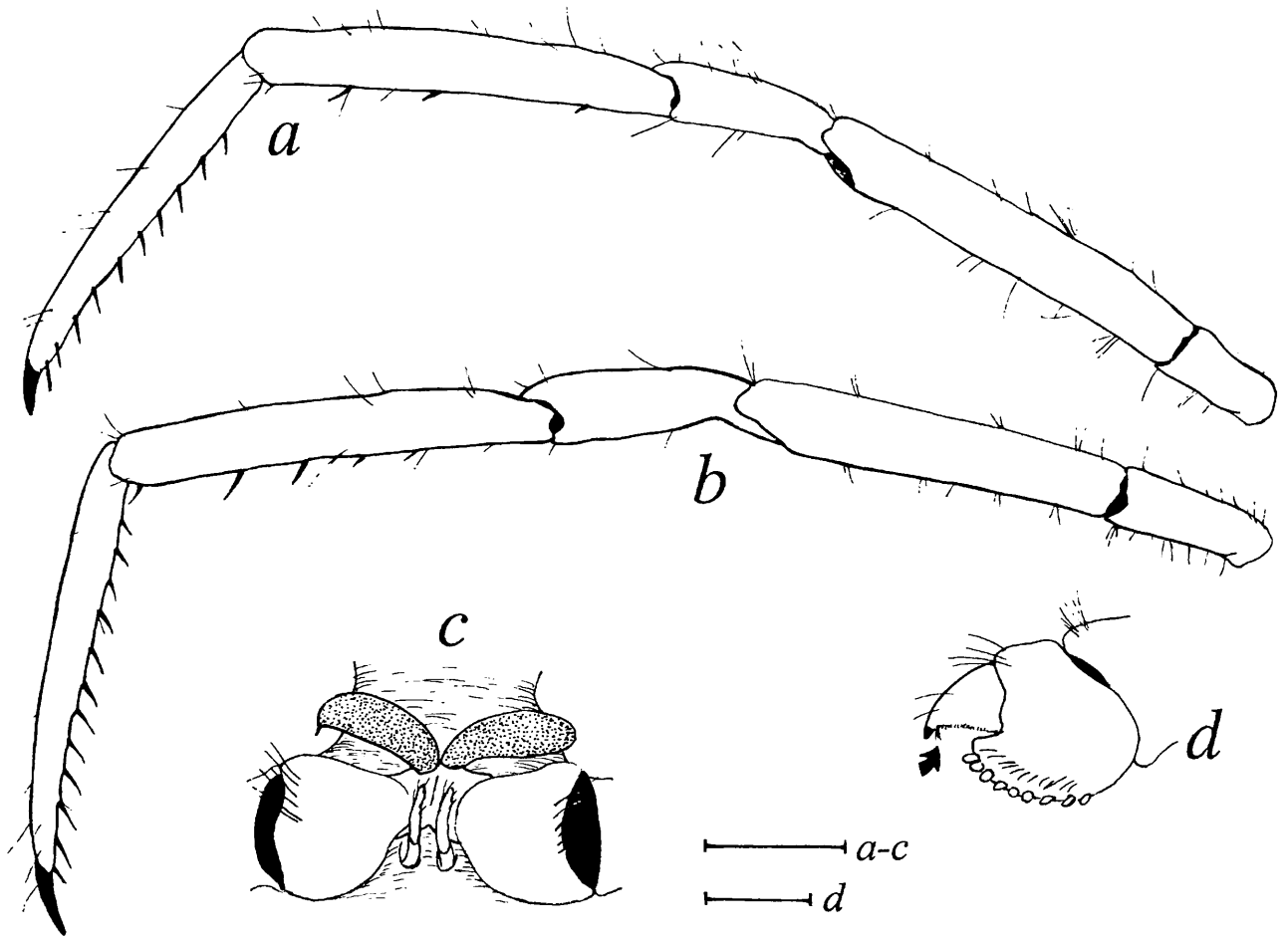


Fig. 2.—*Enallopagurus provenzanoi*, new species, holotype ovig ♀ (sl = 2.40 mm), northwestern Caribbean, R/V *John Elliott Pillsbury*, sta 581, USNM 1007525. a, left second pereopod, lateral; b, left third pereopod, lateral; c, coxae and sternite of fifth pereopods with capsulate setae (stippled), and part of abdomen (lower) showing first pleopods; d, propodus and dactyl of left fourth pereopod with preungual process (arrow), lateral. Scales equal 1.00 mm (a, b), 0.50 mm (c), and 0.10 mm (d).

**Distribution.**—Known at present only from the type locality, off Arrowsmith Bank, in the northwestern Caribbean; 146–265 m.

**Etymology.**—This species is named for Dr. Anthony J. Provenzano, Jr., whose pioneering work on western Atlantic hermit crabs provided the basis for the study of the “*Pylopagurus-Tomopagurus*” group of genera.

**Remarks.**—As previously indicated, *Enallopagurus provenzanoi*, new species, is the first recognized representative of the genus in the western Atlantic. Unlike some species of *Phimochirus* (another of the “*Pylopagurus-Tomopagurus*” group of genera), which is represented in both oceans by geminate pairs (cf. McLaughlin 1981b), *E. provenzanoi* appears to be related to the two

eastern Pacific species only through major generic characters.

Key to Species of *Enallopagurus*

1. Dorsoproximal margin of right chela armed with strong spines; eastern Pacific ..... *E. coronatus*
- Dorsoproximal margin of right chela unarmed ..... 2
2. Dorsal surface of palm of right chela with relatively closely-spaced small spines or spinules; eastern Pacific ..... *E. affinis*
- Dorsal surface of palm of right chela unarmed or rarely slightly tuberculate ... 3
3. Carpus of right cheliped with two or three spines on dorsomesial margin separated by concavity from prominent dorsodistal spine; eastern Pacific ..... *E. spinicarpus*



- Carpus of right cheliped with unarmed dorsomesial margin; Caribbean Sea . . .  
 . . . . . *E. provenzanoi*, new species

*Enallopaguropsis* McLaughlin, 1981a

*Pylopagurus*: Walton, 1954:140 (in part).—Scanland & Hopkins, 1969:257 (in part) [Not *Pylopagurus* A. Milne-Edwards & Bouvier, 1891].

*Enallopaguropsis* McLaughlin 1981a:7; 1982:848; 2003:121.

*Emended diagnosis*.—Eleven pairs of biserial gills. Ocular acicle acutely triangular, with moderate to well-developed submarginal spine. Sternite of third maxillipeds with prominent spine on either side of midline. Third maxilliped with well-developed crista dentata and 1 accessory tooth. Maxillule with internal lobe of endopod moderately well-developed, and with 1 stiff bristle terminally; posterior lobe somewhat produced, not recurved.

Right cheliped with suboperculate chela. Left chela subtriangular in cross-section, but dorsal surface not produced into prominent keel or crest. Dorsodistal spine of carpi of second and third pereopods lacking. Anterior lobe of sternite of third pereopods represented by 1 or 2 capsulate setae. Sternites of fourth and fifth pereopods often with 1 to several large capsulate setae. Fourth pereopod with propodal rasp consisting of multiple rows of corneous scales.

Males with paired gonopores, no distinct sexual tubes but occasionally with vas deferentia produced to form short tubular papillae on one or both coxae; no paired pleopods; 3 unpaired left pleopods with endopods reduced or absent. Females with paired gonopores, paired first pleopods modified as gonopods, 4 unpaired left pleopods, second to fourth with both rami well-developed, fifth with endopod reduced or absent.

Abdomen straight or slightly flexed, usually moderately long; uropods symmetrical or asymmetrical. Telson without indication of division into anterior and posterior por-

tions; terminal margin convex, entire or with shallow median concavity, unarmed.

*Remarks*.—The original diagnosis of *Enallopaguropsis* indicated that the terminal margin of the telson was entire in all the species. In the new species described herein, however, the terminal margin is divided into nearly symmetrical lobes by a shallow median concavity, and the diagnosis of the genus has been corrected accordingly.

With the addition of the new species of *Enallopaguropsis* described herein, the genus is now represented by two eastern Pacific and one western Atlantic species. An updated key to the species is provided following the description of this new species.

***Enallopaguropsis williamsi*, new species**  
Figs. 3, 4

*Holotype*.—♂ (sl = 1.70 mm), R/V *John Elliott Pillsbury*, sta 421, 09°32.1'N, 78°33.5'W, Golfo de San Blas, Panamá, 53–58 m, 19 Jul 1966, USNM 1007523.

*Description*.—Shield (Fig. 3a) longer than broad; anterior margin between rostrum and lateral projections slightly concave; anterolateral margins sloping; posterior margin truncate, dorsal surface with few setae. Rostrum triangular, with terminal spinule. Lateral projections triangular, each with terminal spine or spinule.

Ocular peduncle approximately 0.85 length of shield, moderately stout, with cornea slightly dilated. Ocular acicles subtriangular, each terminating subacutely, with well-developed submarginal spine; separated basally by slightly more than basal width of 1 acicle.

Antennular peduncle overreaching ocular peduncle by approximately 0.50 length of ultimate segment; ultimate and penultimate segments unarmed; basal segment unarmed.

Antennal peduncle slightly shorter than equaling length of ocular peduncle. Fifth and fourth segments with scattered setae. Third segment with acute spine at ventrodistal angle. Second segment with dorsolateral distal angle prominently produced, ter-

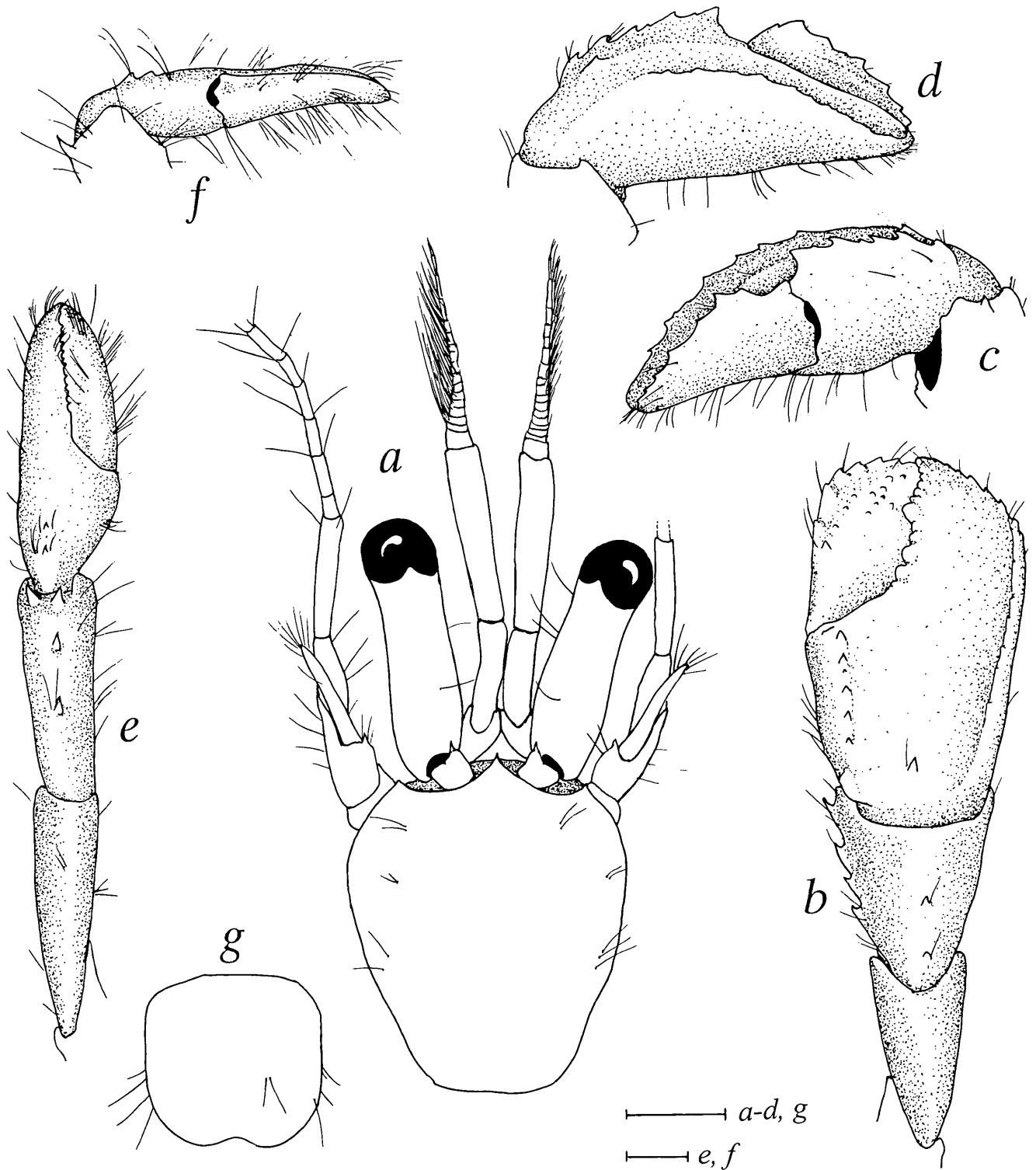


Fig. 3.—*Enallopaguropsis williamsi*, new species, holotype ♂ (sl = 1.70 mm), southwestern Caribbean, R/V John Elliott Pillsbury, sta 421, Golfo de San Blas, Panamá, USNM 1007523. a, shield and cephalic appendages (right antennal flagellum missing), dorsal; b, right cheliped, dorsal; c, chela of same, mesial; d, same, lateral; e, left cheliped, dorsal; f, chela of same, mesial; g, telson, dorsal. Scales equal 0.50 mm (a–d, g) and 0.25 mm (e, f).

minating in small spine; dorsomesial distal angle with small spine. First segment produced ventrally and with acute spine on ventrolateral margin distally. Antennal acicula moderately short, reaching only to distal

margin of fourth peduncular segment. Flagellum with short setae  $\geq 1$  article in length in most articles, and moderately long setae 2 or 3 articles in length every 2 articles.

Right cheliped (Figs. 3b–d) with subop-

erculate chela. Dactyl approximately 0.80 length of palm, approximately equal to fixed finger in width, with row of spines on distal 0.75 of elevated dorsomesial margin, dorsal surface with few small tubercles in distal half; cutting edge with row of moderately large teeth; mesial, lateral and ventral surfaces with scattered short setae. Palm slightly exceeding length of carpus; dorsal surface weakly convex, armed with only 1 small spine slightly mesiad of midline in proximal half, elevated dorsomesial margin forming spinose crest, dorsolateral margin also elevated as low ridge proximally becoming more pronounced and weakly serrate distally and on fixed finger; cutting edge of fixed finger with row of distinct teeth; mesial, lateral and ventral surfaces with sparse tufts of setae. Carpus approximately equal to length of merus, subtrapezoidal; dorsomesial margin with row of 4 prominent spines, dorsolateral margin not delimited, dorsal surface with longitudinal row of 2 spinose protuberances proximally, otherwise surfaces unarmed, but with few scattered setae. Merus triangular, margins and surfaces unarmed but with scattered, short setae. Ischium unarmed.

Left cheliped (Figs. 3e, f) with dactyl approximately as long as palm; surfaces of dactyl and fixed finger unarmed but with sparse tufts of setae, dorsal surface of palm with 2 small spines in midline proximally. Carpus only slightly shorter than merus; dorsal surface with longitudinal row of 2 spines medially, and 2 additional spines on distal margin; mesial, lateral and ventral surfaces unarmed but with few scattered setae. Merus and ischium with only scattered short to moderately long setae on all surfaces.

Second and third pereopods (Figs. 4a, b) moderately long and slender. Dactyls equal to or slightly longer than propodi; dorsal surfaces with few short setae; ventral margins each with row of 6 or 7 long corneous spines and few short setae. Propodi approximately 1.50 to nearly twice as long as carpi; dorsal surfaces with few setae; with 1

or 2 ventrodiscal spiniform bristles, and 1 or 2 additional slightly shorter spiniform bristles on each ventral margin distally. Carpi 0.45–0.75 length of meri, unarmed, but with scattered setae dorsally and ventrally. Meri and ischia unarmed, but with dorsal and ventral sparse tufts of setae.

Fourth pereopod (Fig. 4d) with propodal rasps consisting of 3 rows of corneous scales. Dactyl lacking preungual process.

Sternites of third, fourth, and fifth pereopods (Fig. 4c) each with 3, 4, and 2 capsulate setae, respectively. Coxae of fifth pereopods with vas deferentia slightly produced forming short tubular papillae on right and left sides (Fig. 4c).

Uropods nearly symmetrical. Telson (Fig. 3g) without indications of division into anterior and posterior portions; terminal margin with broad median concavity, unarmed.

*Color*.—Shield weakly mottled orange with large darker orange spot on each side laterally and few smaller spots and patches in distal half. Ocular peduncles mottled light orange with scattered darker orange specks. Antennal peduncles with band of light orange on second segments superimposed with few darker orange specks; antennal acicles with few patches of light orange. Chelipeds each generally light orange with few scattered darker orange patches; dactyls each with proximal darker orange band. Dactyls of second and third pereopods each with orange band in proximal half; propodi with scattered orange spots and orange band at mid-length; carpi very light orange, that of third with at least scattered darker orange specks; meri faint orange, darker proximally and with numerous darker orange specks. (From notes by B. Stolen, artist for A. J. Provenzano, Jr.)

*Etymology*.—This species is dedicated to the memory of Dr. Austin B. Williams (1919–1999, see Lemaitre & Collette 2000), esteemed colleague who during many years of work at the Systematics Laboratory, National Marine Fisheries Service, contributed greatly to our knowledge of western Atlantic decapod crustaceans.

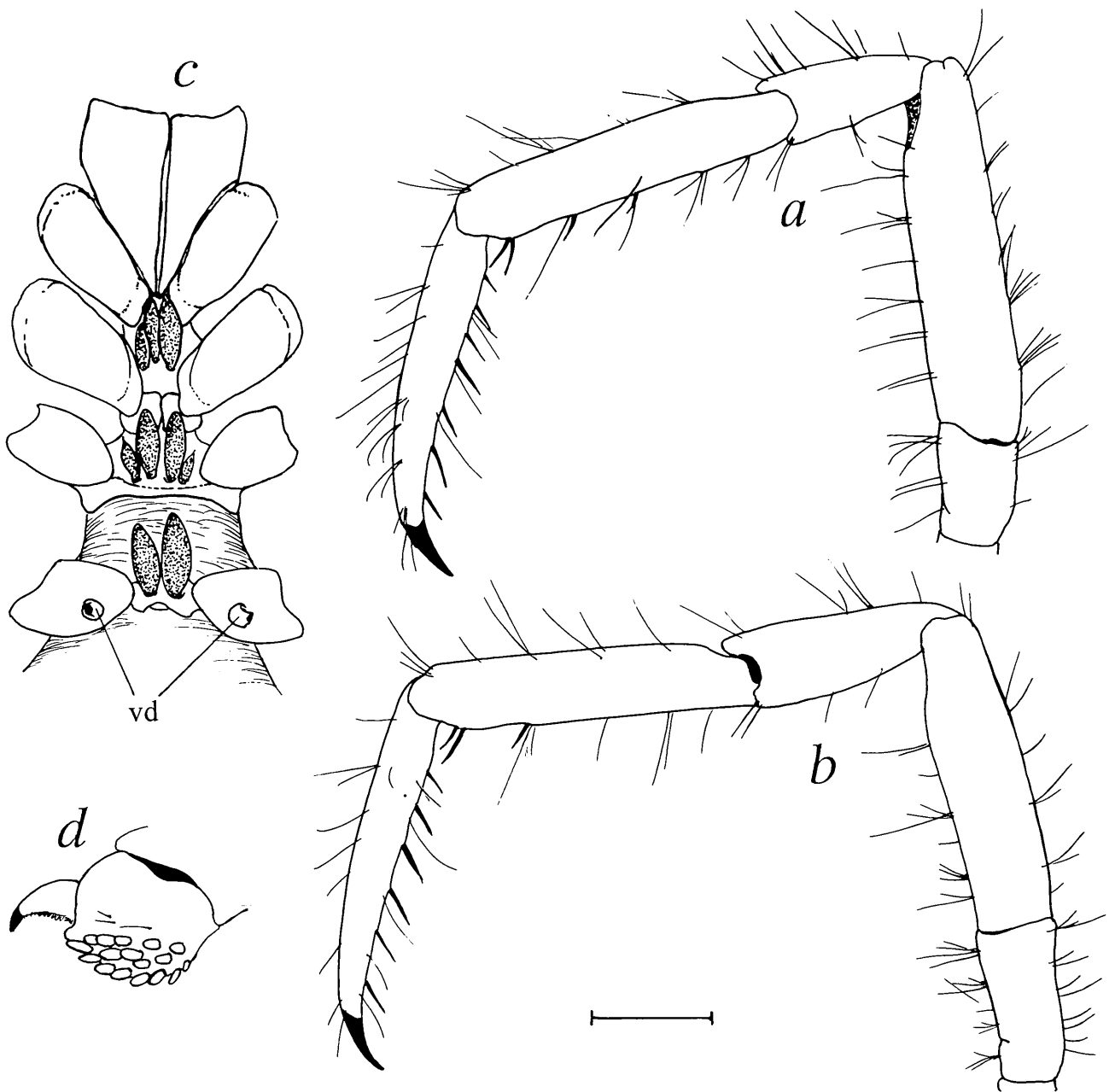


Fig. 4.—*Enallopaguropsis williamsi*, new species, holotype ♂ (sl = 1.70 mm), southwestern Caribbean, R/V *John Elliott Pillsbury*, sta 421, Golfo de San Blas, Panamá, USNM 1007523. a, left second pereopod, lateral; b, left third pereopod, lateral; c, coxae and sternites of first to fifth pereopods with capsulate setae (stippled), and protruded vas deferens (vd), ventral; d, propodus and dactyl of left fourth pereopod, lateral. Scale equals 0.50 mm (a–c) and 0.25 mm (d).

*Habitat*.—Housing unknown. Bottom where found consisted of “coralline plates and broken shells” (Voss 1966).

*Distribution*.—Known only from the type locality, Golfo de San Blas, on the Caribbean coast of Panamá.

*Remarks*.—Because *Enallopaguropsis williamsi*, new species, is known from only the male holotype, this species can only provisionally be assigned to *Enallopagu-*

*ropsis*. The telson of *E. williamsi* bears some resemblance to species of *Agaricochirus*. However, the morphology of the right cheliped and propodal rasp suggests that this new species belongs in *Enallopaguropsis*.

Key to Species of *Enallopaguropsis*

- 1. Palm of left chela with row of spines on dorsolateral margin ..... 2

- Palm of left chela with unarmed dorso-lateral margin; Caribbean Sea . . . . .  
   . . . . . *E. williamsi*, new species
- 2. Dorsal surface of right chela covered with closely-spaced corneous-tipped spinules or granules; eastern Pacific . . . . .  
   . . . . . *E. guatemoci*
- Dorsal surface of right chela with scattered tubercles; eastern Pacific . . . . .  
   . . . . . *E. janetae*

*Phimochirus randalli* (Provenzano, 1961)  
 Figs. 5–7

*Pylopagurus randalli* Provenzano, 1961: 159, fig. 2 (type locality: ridge 5 miles southeast of Lameshur Bay, St. John, Virgin Islands).

*Phimochirus randalli*: McLaughlin, 1981a: 5; 1981b:340, figs. 4b, 5b, 7b.—Williams et al., 1989:32.—McLaughlin et al., 2003:125.

*Holotype*.—♂ (sl = 6.20 mm), SE Lameshur Bay, St. John, Virgin Islands, 20 m, 5 Feb 1960, colls. J. Randall and T. Chess, USNM 106353.

*Material examined*.—Northern Gulf of Mexico, R/V *Pelican*, U.S. Department of Energy project: 1 ♂ (sl = 6.70 mm) + exuvia, 27°48.717'N, 93°02.880'W, dredged at night, calcareous rubble, 16 Aug 1998, USNM 276157 (photo voucher).—1 ♀ ovig (sl = 5.9 mm), dredge sta 10-3, 28°05.999'N, 91°02.289'W, 57 m, 27 May 2000, ULLZ 4678 (photo voucher).—1 ♂ (sl = 2.80 mm), dredge sta 7-2, 91°02.481'W, 57–60 m, 1 Jul 2001, ULLZ 4551 (photo voucher).

*Diagnosis*.—Shield (Fig. 5a) longer than broad; dorsal surface with several short transverse or oblique rows of bristle-like setae; rostrum prominent, acutely triangular; with minute terminal spine; lateral projections obsolete or broadly triangular, usually with minute terminal spine. Ocular peduncles stout, about 0.60 times length of shield, with corneas strongly dilated. Ocular acicles elongate, acutely triangular; dorsal surfaces concave distally; each usually with

small, submarginal spine terminally; separately basally by basal width of 1 acicle.

Antennular peduncle exceeding distal margin of cornea by about 0.30 length of ultimate segment. Antennal peduncle exceeding distal margin of cornea by about 0.30 length of fifth segment; second segment with dorsolateral distal angle produced, terminating in strong spine, dorsomesial distal angle with small spine; first segment unarmed; acicle elongate, weakly arcuate, reaching to about midpoint of fifth antennal segment, terminating in spine, unarmed. Antennal flagella moderately long; with short setae every 3 or 4 articles, each seta about 1 flagellar article in length.

Right cheliped (Fig. 6) sparsely setose. Chela operculate, dorsoventrally compressed (more markedly so laterally and mesially); dorsal surfaces of palm and fingers covered with low, mushroom-like tubercles replaced medially on palm by 2 longitudinal, rectangular or ovate granular patches separated by narrow tuberculate area; patches slightly depressed, with granules arranged in irregular, transverse rows. Fixed finger broad basally, with up to 6 blunt spines dorsally more prominent than surrounding tubercles. Dactyl about as long or slightly shorter than length of palm; mesial margin with blunt spines; dorsal surface with 2 (1 distal, 1 proximal) blunt spines standing out from surrounding tubercles. Carpus with granules or low tubercles on dorsal, lateral and mesial surfaces, dorsomesial margin with row of irregular, corneous-tipped spines; mesial surface concave distally. Merus with row of small spines or spinulose tubercles on ventromesial and ventrolateral margins; dorsodistal margin with row of 4–6 corneous-tipped spines.

Left cheliped (Fig. 5b) with surfaces of carpus and chela usually covered with small, flattened tubercles or granules. Palm with longitudinal, often ridge-like elevation in midline armed with row of spines or spinules, and flanked on each side by subrectangular or ovate area nearly smooth or with

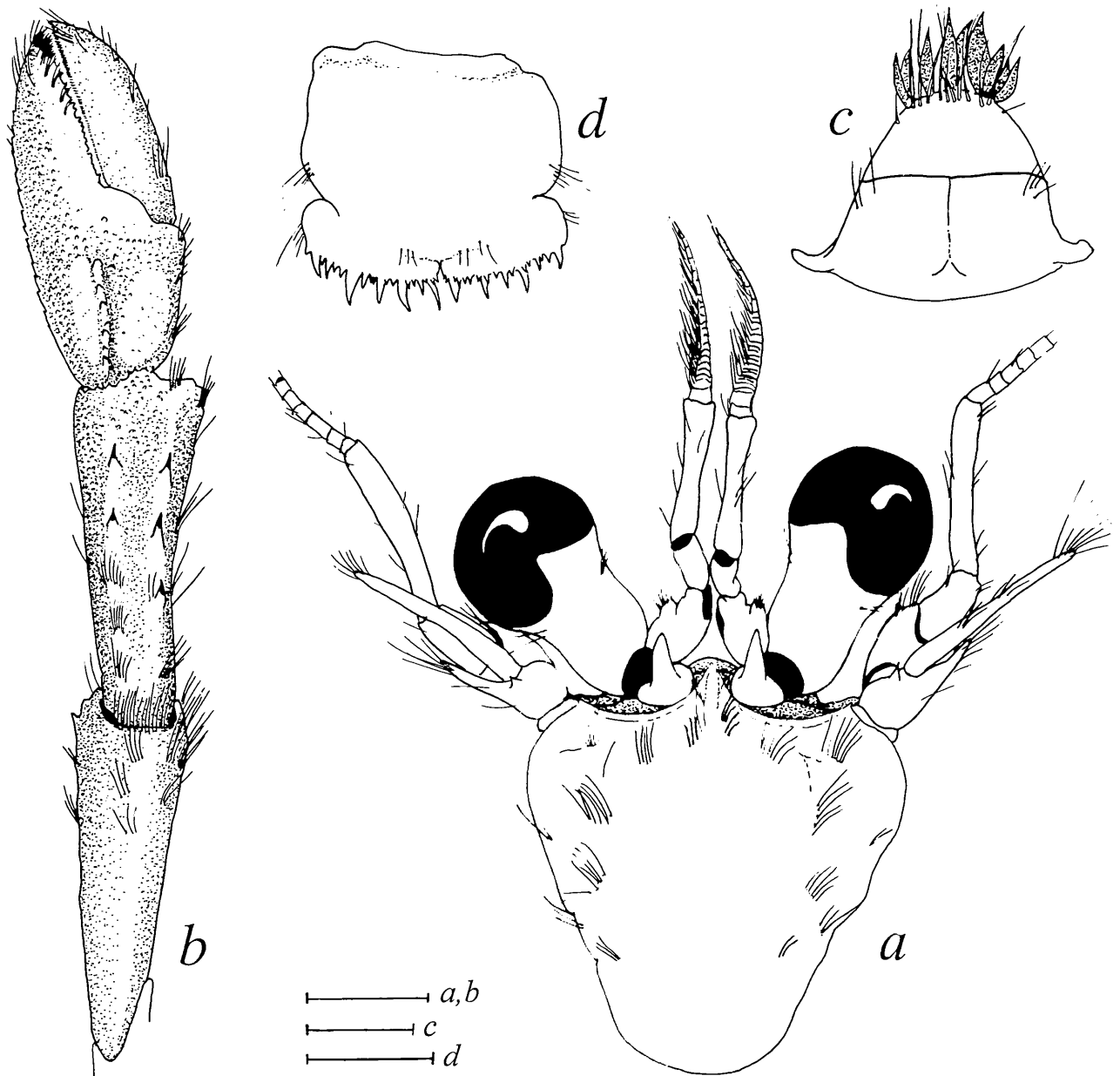


Fig. 5.—*Phimochirus randalli* (Provenzano, 1961), northern Gulf of Mexico, R/V *Pelican*, M (sl = 6.70 mm), USNM 276157. a, shield and cephalic appendages, dorsal; b, left cheliped, dorsal; c, sternite of third pereopods, ventral; d, telson, dorsal. Scales equal 2.00 mm (a, b), and 1.00 mm (c, d).

scattered small granules. Carpus with dorsolateral and dorsomesial margins each with irregular row of 2–4 corneous-tipped spines; dorsodistal margin minutely spinulose.

Second and third pereopods (Fig. 7a–d) with meri, carpi, propodi and dactyls setose dorsally. Dactyls moderately short, about 1.20–1.40 times as long as dorsal margins of propodi; dorsal and dorsomesial distal margins with small corneous spines interspersed with setae; ventral margins each with row of 7–9 corneous spines. Propodi

with dorsal surfaces spinulose or tuberculate, ventral margins each with row of 2–4 corneous spines in addition to pair of corneous spines on distal angle. Carpi each with prominent dorsodistal spine.

Fourth pereopod (Fig. 7e) with distinct preungual process on dactyl surrounded by dense, circularly arranged setae.

Sternite of third pereopods (Fig. 5c) with subquadrate to semicircular anterior lobe; sternites of third to fifth pereopods frequently with capsulate setae.

Telson (Fig. 5d) with distinct transverse





Fig. 6.—*Phimochirus randalli* (Provenzano, 1961), northern Gulf of Mexico, R/V *Pelican*, M (sl = 6.70 mm), USNM 276157. Right cheliped ( $\times 3.97$ ).

indentation; terminal margin nearly straight or broadly rounded, divided into left and right lobes by V-shaped cleft, each portion armed with several elongate spines interspersed with shorter spines.

*Color*.—Generally amber or brownish. Anterior half of shield mottled with white patches. Branchiostegites with white patches surrounded by brownish to purple. Ocular peduncles with irregular white patches basally, turning to uneven tints of amber distally; each peduncle with distinct, light purple spot on dorsomesial surface near cornea. Basal segments of antennules purple, penultimate segments and flagella white, remaining parts amber or brownish. Right cheliped amber or brownish except for few white spines on dorsal surface of fingers and dorsodistal surface of carpus; carpus with band of white patches on dorsal

surface proximally; merus with band of white patches surrounded by light purple tint on dorsodistal surface. Left cheliped also amber or brownish except for scattered white patches on carpus; merus similar in color to that of right cheliped. Second and third pereopods with distal halves of dactyls white and amber proximally; propodi white on distal thirds, with white patches proximally, otherwise amber; carpi each with white dorsodistal spine having light purplish tint basally, elsewhere with scattered white patches over amber; meri with many white patches on lateroventral surfaces surrounded by light purplish tint, otherwise amber. Fourth and fifth pereopods amber with white patches. (Based on photographs of live specimens taken by D. L. Felder).

*Habitat*.—Found in gastropod shells. According to Provenzano (1961) the holotype was found in a shell of the gastropod *Semicassis granulata* (Born).

*Distribution*.—Bahama Islands; Straits of Florida; northern Gulf of Mexico; eastern and western Caribbean. Depth: 15–91 m.

*Remarks*.—McLaughlin's (1981b:340, fig. 5b) diagnosis and illustration of the right chela of *P. randalli* describe a median "ridge" that separates two longitudinal, slightly depressed, granular patches. This "ridge" was used by McLaughlin (1981b:336, couplet 1) in her key to separate *P. randalli* from all other congeners. Based on the study of the Gulf of Mexico specimens herein reported, and a reexamination of some of the specimens used by McLaughlin (1981b), we have found that the use of this ridge as a key diagnostic character may lead to confusion. In some individuals the ridge does appear somewhat elevated as result of the two depressed patches, whereas in others the patches are hardly if at all depressed, and no distinct ridge is apparent. Actually, it is the presence of granular patches that more clearly serve to separate *P. randalli* from other congeners. The tubercles that cover the other portions of the dorsal surface of the right palm can also vary in strength and size. Given the variation ob-

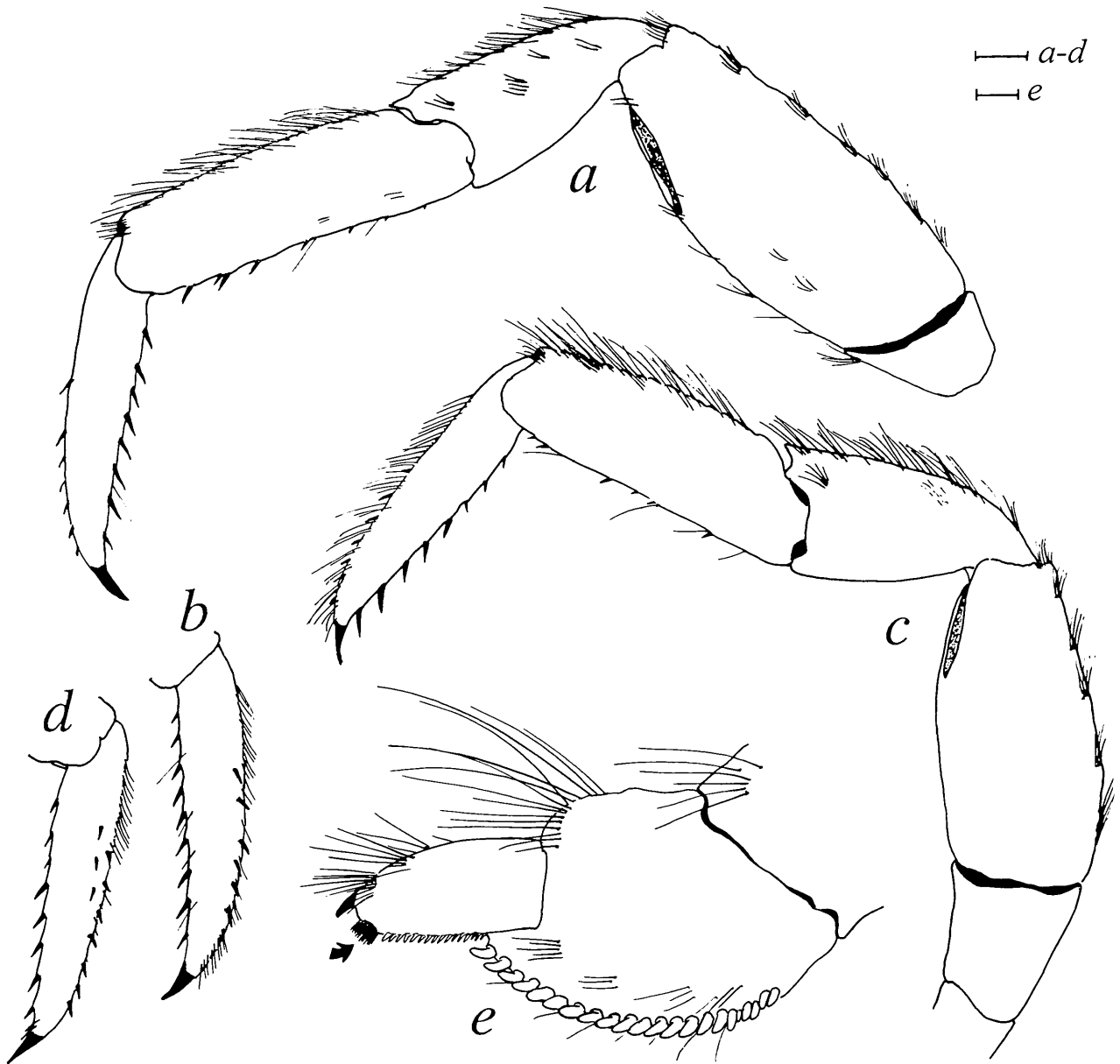


Fig. 7.—*Phimochirus randalli* (Provenzano, 1961), northern Gulf of Mexico, R/V *Pelican*, ♂ (sl = 6.70 mm), USNM 276157. a, left second pereopod, lateral; b, dactyl of same, mesial; c, left third pereopod, lateral; d, dactyl of same, mesial; e, propodus and dactyl of left fourth pereopod with preungual process (arrow), lateral. Scales equal 0.50 mm (a–d) and 0.25 mm (e).

served on the right palm of *P. randalli*, which requires a modification of couplet 1 of McLaughlin's (1981b) key, and the removal by McLaughlin (1988) of *Phimochirus liochele* to *Pagurus*, an updated key to the species is presented.

Updated Key to Species of *Phimochirus*

- 1. Palm of right chela with two longitudinal, rectangular or ovate granular patches; western Atlantic . . . . . *P. randalli*
- Palm of right chela without longitudinal granular patches . . . . . 2

- 2. Dorsal surface of dactyl of right chela with median ridge or row of tubercles or spines . . . . . 3
- Dorsal surface of dactyl of right chela without median ridge or row of tubercles or spines . . . . . 7
- 3. Dorsal surface of palm and fixed finger of right chela with strong or moderately strong tubercles, at least distally . . . . . 4
- Dorsal surface of palm and fixed finger of right chela smooth, granular or weakly tuberculate . . . . . 5
- 4. Exopod of left uropod with dense tuft of long setae; eastern Pacific . . . . .
- . . . . . *P. californiensis*



- Exopod of left uropod without dense tuft of long setae; western Atlantic . . . . . *P. holthuisi*
- 5. Dorsal surface of carpus of right cheliped unarmed; western Atlantic . . . . . *P. leurocarpus*
- Dorsal surface of carpus of right cheliped tuberculate, spinose or spinulose . . . . . 6
- 6. Palm of left chela with dorsal midline unarmed or with few spinules or tubercles proximally; eastern Pacific . . . . . *P. venustus*
- Palm of left chela with dorsomedial row of small spines or tubercles extending to base of dactyl; western Atlantic . . . . . *P. operculatus*
- 7. Exopod of left uropod with dense tuft of long setae; eastern Pacific . . . . . *P. roseus*
- Exopod of left uropod without dense tuft of long setae; western Atlantic . . . . . *P. oclusus*

Taxonomic Summary of the  
“*Pylopagurus-Tomopagurus*” Group of  
Taxa, from the Publication of Part 1 in  
1981 to the Present

(Taxa listed in same order discussed during revision of group; see Table 1 for list of current valid names)

Genus *Tomopagurus* A. Milne-Edwards & Bouvier, 1893

*Species assigned by McLaughlin (1981a).*—*Tomopagurus rubropunctatus* A. Milne-Edwards & Bouvier, 1893, *T. cokeri* (Hay, 1917), *T. maclaughlinae* Haig, 1976, *T. cubensis* (Wass, 1963), *T. wassi* McLaughlin, 1981a, *Pagurus purpuratus* (Benedict, 1892), *P. merimaculosus* Glassell, 1937, and *Pylopagurus chacei* Wass, 1963.

*Changes and additions since McLaughlin (1981a).*—None.

*Species discussion.*—See McLaughlin (1981a).

Genus *Rhodochirus* McLaughlin, 1981a

*Species assigned by McLaughlin (1981a).*—*Pylopagurus rosaceus* A. Milne-Edwards & Bouvier, 1893, *Pylopagurus*

*hirtimanus* Faxon, 1893. McLaughlin (1981a) also considered *P. acutus* Forest & de Saint Laurent, 1968, a synonym of *Rhodochirus rosaceus*.

*Changes and additions since McLaughlin (1981a).*—None.

*Species discussion.*—See McLaughlin (1981b).

Genus *Phimochirus* McLaughlin, 1981a

*Species assigned by McLaughlin (1981a).*—*Pylopagurus operculatus* (Stimpson, 1859), *P. californiensis* (Benedict, 1892), *P. mexicanus* (Benedict, 1892), *P. venustus* (Bouvier, 1898), *P. roseus* (Benedict, 1892), *P. randalli* Provenzano, 1961, and *P. holthuisi* Provenzano, 1961. Questionably assigned were *P. oclusus* (Henderson, 1888) and *P. liochele* Barnard, 1947.

*Changes and additions since McLaughlin (1981a).*—McLaughlin (1981b:349) synonymized *Pylopagurus mexicanus* with *Phimochirus californiensis*, and described *P. leurocarpus*. McLaughlin (1988:6) transferred *Phimochirus liochele* to *Pagurus*.

*Species discussion.*—See McLaughlin (1981b, 1988), and this study.

Genus *Agaricochirus* McLaughlin, 1981a

*Species assigned by McLaughlin (1981a).*—*Pylopagurus boletifer* A. Milne-Edwards & Bouvier, 1893, *P. alexandri* A. Milne-Edwards & Bouvier, 1893, *P. cavimanus* Chace, 1939, *P. erosus* (A. Milne-Edwards, 1880), *P. gibbosimanus* (A. Milne-Edwards, 1880), and *Pagurus hispidus* (Benedict, 1892).

*Changes and additions since McLaughlin (1981a).*—McLaughlin (1982:838, 841) described *Agaricochirus acanthinus* and *A. echinatus*.

*Species discussion.*—See McLaughlin (1982).

Genus *Enallopagurus* McLaughlin, 1981a

*Species assigned by McLaughlin (1981a).*—*Pylopagurus spinicarpus* Glas-

sell, 1938, *P. affinis* Faxon, 1893, and *P. coronatus* (Benedict, 1892).

*Changes and additions since McLaughlin (1981a).*—*Enallopagurus provenzanoi* is described in this study.

*Species discussion.*—See McLaughlin (1982), and this study.

Genus *Enallopaguropsis* McLaughlin,  
1981a

*Species assigned by McLaughlin (1981a).*—*Pylopagurus guatemoci* Glassell, 1937, and *P. hancocki* Walton 1954.

*Changes and additions since McLaughlin (1981a).*—McLaughlin (1982:849, 851) synonymized *Enallopaguropsis hancocki* with *E. guatemoci*, and described *E. janetae*. *Enallopaguropsis williamsi* is described in this study.

*Species discussion.*—See McLaughlin (1982), and this study.

Genus *Lophopagurus* McLaughlin, 1981a

*Species assigned by McLaughlin (1981a).*—*Pylopagurus thompsoni* (Filhol, 1885), *P. lacertosus* (Henderson, 1888), *P. nanus* (Henderson, 1888), *P. crenatus* (Borradaile, 1916), and questionably *P. cristatus* (H. Milne Edwards, 1836).

*Changes and additions since McLaughlin (1981a).*—McLaughlin & Gunn (1992:52, 55) described *Lophopagurus foresti*, and *L. nodulosus*; de Saint Laurent & McLaughlin (2000:150) described *L. pumilus*.

De Saint Laurent & McLaughlin (2000:148) reduced McLaughlin's (1981a) genus *Australeremus* to subgeneric status within *Lophopagurus*. The subgenus *Lophopagurus* then became the nominal subgenus. The following species were assigned by de Saint Laurent & McLaughlin (2000:149) to *Lophopagurus (Lophopagurus)*: *L. (L.) foresti*, *L. (L.) lacertosus*, *L. (L.) nanus*, *L. (L.) nodulosus*, *L. (L.) pumilus*, and *L. (L.) thompsoni*. De Saint Laurent & McLaughlin (2000:153) also synonymized *L. (L.) crenatus* with *L. (L.) lacertosus*.

*Species discussion.*—See McLaughlin &

Gunn (1992), and de Saint Laurent & McLaughlin (2000).

Genus *Australeremus* McLaughlin, 1981a

*Species assigned by McLaughlin (1981a).*—*Pylopagurus cooki* (Filhol, 1883), and *P. kirki* (Filhol, 1883).

*Changes and additions since McLaughlin (1981a).*—McLaughlin & Gunn (1992:68) assigned *Pylopagurus stewarti* and *P. serpulophilus* to *Australeremus*, and considered the latter species a junior synonym of *Australeremus triserratus* (Ortmann, 1892). McLaughlin & Gunn (1992:74, 77, 92) also described *Australeremus laurentae* and *A. eltaninae*, and added *A. cristatus* (H. Milne Edwards, 1836).

McLaughlin's (1981a) genus *Australeremus* was reduced by de Saint Laurent & McLaughlin (2000:148) to subgeneric rank within *Lophopagurus*. The following species were assigned by de Saint Laurent & McLaughlin (2000:166) to *Lophopagurus (Australeremus)*: *L. (A.) cookii* [also corrected spelling], *L. (A.) eltaninae*, *L. (A.) cristatus*, *L. (A.) kirkii* [also corrected spelling], *L. (A.) laurentae*, *L. (A.) stewarti*, and *L. (A.) triserratus*.

*Species discussion.*—See McLaughlin & Gunn (1992), and de Saint Laurent & McLaughlin (2000).

Genus *Anisopagurus* McLaughlin, 1981a

*Species assigned by McLaughlin (1981a).*—*Pylopagurus bartletti* A. Milne-Edwards, 1880, and *P. pygmaeus* (Bouvier, 1918).

*Changes and additions since McLaughlin (1981a).*—Lemaitre & McLaughlin (1996:95, 101, 108) described *Anisopagurus actinophorus*, *A. hopkinsi*, and *A. vossi*.

*Species discussion.*—See Lemaitre & McLaughlin (1996).

Genus *Manucomplanus* McLaughlin,  
1981a

*Species assigned by McLaughlin (1981a).*—*Pylopagurus corallinus* (Bene-

dict, 1892), *P. cervicornis* (Benedict, 1892), *P. spinulosus* Holthuis, 1959, *P. longimanus* Faxon, 1893, *P. varians* (Benedict, 1892), and questionably *P. unguatus* (Studer, 1883).

*Changes and additions since McLaughlin (1981a).*—Lemaitre & McLaughlin (1996: 113) synonymized *Manucomplanus coralinus* with *M. unguatus*.

*Species discussion.*—See Lemaitre & McLaughlin (1996).

Genus *Protoniopagurus* Lemaitre & McLaughlin, 1996

*Species assigned.*—Monotypic: *Protoniopagurus bioperculatus* Lemaitre & McLaughlin, 1996.

*Species discussion.*—See Lemaitre & McLaughlin (1996).

Genus *Pylopagurus* A. Mine-Edwards & Bouvier, 1891 *sensu stricto*

*Species assigned by McLaughlin (1981a).*—*Pylopagurus discoidalis* (A. Milne-Edwards, 1880), *P. holmesi* Schmitt, 1921, *P. longicarpus* Walton, 1954, *P. stewarti* (Filhol, 1883), and *P. serpulophilus* Miyake, 1978.

*Changes and additions since McLaughlin (1981a).*—As mentioned under *Australeremus*, McLaughlin & Gunn (1992:68) transferred *Pylopagurus stewarti* and *P. serpulophilus* to *Australeremus* McLaughlin, 1981a, and considered the latter species a junior synonym of *A. triserratus* (Ortmann, 1892).

*Pylopagurus longicarpus* was shown to be a junior synonym of *P. holmesi* by McLaughlin & Lemaitre (2001:459).

Lemaitre & Campos (1993:554) described *Pylopagurus pattiae*, and McLaughlin & Lemaitre (2001:464, 468) described *P. macgeorgei* and *P. gorei*.

*Species discussion.*—See Lemaitre & Campos (1993), and McLaughlin & Lemaitre (2001).

Genus *Haigia* McLaughlin, 1981a

*Species assigned by McLaughlin (1981a).*—Monotypic: *Pylopagurus diegensis* Scanland & Hopkins, 1969.

*Changes and additions since McLaughlin (1981a).*—None.

*Species discussion.*—See McLaughlin & Lemaitre (2001).

Genus *Pylopaguridium* McLaughlin & Lemaitre, 2001

*Species assigned.*—Monotypic: *Pylopaguridium markhami* McLaughlin & Lemaitre (2001).

*Species discussion.*—See McLaughlin & Lemaitre (2001).

Corrected Key to Genera of the “*Pylopagurus-Tomopagurus*” Group

In light of the morphology of the telson in the new species *Enallopagurus provenzanoi* and *Enallopaguropsis williamsi*, the key provided by McLaughlin & Lemaitre (2001:480) must be modified as follows:

- 1. Abdomen reduced; males without unpaired pleopods; females with unpaired pleopods 2–4 . . . . . *Protoniopagurus*
- Abdomen not reduced; males with some unpaired pleopods; females with unpaired pleopods 2–5 . . . . . 2
- 2. Protopods of uropods prominently produced posteriorly; dorsal surface of right chela commonly with characteristic covering of mushroom-shaped tubercles . . . . . *Agaricochirus*
- Protopods of uropods not prominently produced posteriorly; dorsal surface of right chela usually without characteristic covering of mushroom-shaped tubercles . . . . . 3
- 3. Spines on dorsal surfaces of chelae with basal rosettes . . . . . *Rhodochirus*
- Spines on dorsal surfaces of chelae without basal rosettes . . . . . 4
- 4. Propodal rasps of fourth pereopods each with more than one row of corneous scales . . . . . 5
- Propodal rasps of fourth pereopods

- each with one row of corneous scales ..... 7
- 5. Left chela triangular or subtriangular in cross-section, dactyl and fixed finger not dorsoventrally flattened ..... 6
  - Left chela not triangular or subtriangular in cross-section, dactyl and fixed finger dorsoventrally flattened ..... *Manucomplanus*
- 6. Telson with lateral indentations suggesting division into anterior and posterior portions ..... *Anisopagurus*
  - Telson without lateral indentations suggesting division into anterior and posterior portions ..... *Enallopaguropsis*
- 7. Ocular acicles simple; coxae of male fifth pereopods symmetrical ..... 8
  - Ocular acicles multispinose; coxae of male fifth pereopods asymmetrical ... *Pylopaguridium*
- 8. Telson with lateral indentations suggesting division into anterior and posterior portions ..... 9
  - Telson without lateral indentations suggesting division into anterior and posterior portions ..... *Enallopagurus*
- 9. Chela of right cheliped subovate to subcircular, margins unarmed, weakly tuberculate or minutely crenulate and/or serrate, but never armed with prominent, blunt or acute spines ..... 10
  - Chela of right cheliped variable, margins armed with prominent, blunt or acute spines or tubercles ..... 11
- 10. Fourth pereopods with large, very prominent preungual process at base of claw ..... *Phimochirus*
  - Fourth pereopod without large, very prominent preungual process at base of claw ..... *Pylopagurus*
- 11. Dactyl and fixed finger of left chela excavated ventral, presenting “spoon-shaped” appearance ..... *Tomopagurus*
  - Dactyl and fixed finger of left chela not excavated ventrally and not presenting spoon-shaped appearance ..... 12
- 12. Left cheliped with rotation of propodal-carpal articulation 45°–90° from horizontal plane ..... *Lophopagurus (Australeremus)*
  - Left cheliped with rotation of propodal-carpal articulation much less than 45° from horizontal plane ..... 13

- 13. Left chela with midline elevated into prominent keel or crest ..... *Lophopagurus (Lophopagurus)*
  - Left chela with midline sometimes elevated, but not into prominent keel or crest ..... *Haigia*

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