

Figure 8. Right chelae (a–c) and left chelae (d–f): (a) *Enallopagurus spinicarpus* (6.5×); (b) *Enallopagurus affinis* (14.5×); (c) *Enallopagurus coronatus* (35×); (d) *Enallopagurus spinicarpus* (10.9×); (e) *Enallopagurus affinis* (15.1×); (f) *Enallopagurus coronatus* (56×).

wards and Bouvier (1891, 1893) as *Pylopagurus unguatus* (Studer). As pointed out by McLaughlin (1981a), this taxon is in reality *Manucomplanus corallinus* (Benedict), and any relationship between Faxon's and Benedict's species is superficial, at best. Although females of *E. affinis* have yet to be reported, there is little doubt that this species is properly assigned to *Enallopagurus*.

Enallopagurus coronatus (Benedict, 1892)

Figures 7c, 8c, f

Eupagurus coronatus Benedict, 1892: 24 (type locality: off Cape San Lucas, Gulf of California, ALBATROSS station 2829).—Alcock, 1905: 180.

Pylopagurus coronatus: Glassell, 1937: 254.—Walton, 1954: 149, pl. 43, fig. A.—Gordan, 1956: 340.—Scanland and Hopkins, 1969: 259.

Pagurus coronatus: Gordan, 1956: 328.

Enallopagurus coronatus: McLaughlin, 1981a: 7 (by implication).

Holotype.—♂ (SL = 2.0 mm), USNM 16699.

Material Examined.—See Table 1.

Diagnosis.—Shield as long or slightly longer than broad; rostrum prominent, acutely triangular, with small terminal spine; lateral projections acutely or obtusely triangular, with marginal or submarginal spine. Ocular peduncles moderately long and slender, with corneae slightly dilated; ocular acicles subovate, with moderately strong or strong submarginal spine; separated by less than basal width of 1 acicle. Right cheliped with weakly protuberant crest or ridge on dorsal margin of merus. Carpus with 2 or 3 widely spaced spines on dorsomesial margin, dorsal midline with spinulose longitudinal ridge. Dorsal surface of palm and fixed finger with scattered low tubercles, dorsal margins (mesial, lateral, and proximal) with strong, widely-spaced spines; dorsomesial margin of dactyl spinulose, dorsal surface with few low tubercles. Left cheliped with merus usually unarmed. Carpus with pair of strong spines on dorsodistal margin and 1 spine on mid-dorsolateral margin. Dorsolateral margin of palm and fixed finger with row of low spines; dorsal surface elevated in midline and with 1 or 2 strong spines near proximal margin; dactyl with rows of tufts of long setae. Dactyls of 2nd and 3rd pereopods short, terminating in strong corneous claws; ventral margins of dactyls and propodi each with row of corneous spines, dorsal and ventral margins with tufts of setae. Sternite of 3rd pereopods with anterior lobe narrowly subovate. Uropods symmetrical. Telson not subdivided into anterior and posterior lobes; terminal margin entire, convex, unarmed.

Distribution.—Gulf of California, Mexico; 57–137 m.

Remarks.—*E. coronatus* is easily distinguished from the other species of the genus by the armature of the right chela. Strong marginal spines encircle the entire palm and lateral portion of the fixed finger in this species.

Enallopaguropsis McLaughlin, 1981

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

Enallopaguropsis McLaughlin, 1981a: 7. Type species, by original designation: *Pylopagurus guatemoci* Glassell, 1937. Gender: feminine.

Diagnosis.—Eleven pairs of phyllobranch gills. Ocular acicles acutely triangular, with moderately well developed submarginal spine; separated basally by approximate basal width of 1 acicle. Sternite of 3rd maxillipeds with strong spine on either side of midline. Third maxillipeds each with well developed crista dentata with prominent accessory tooth; merus with spine at dorsodistal margin. Maxillule with internal lobe of endopod moderately well developed and with 1 stiff bristle terminally; external lobe moderately well developed, not recurved.

Right cheliped with chela suboperculate; angle of articulation approximately perpendicular. Left chela subtriangular in cross-section, but without prominent keel or crest; angle of articulation of chela and carpus approaching 60° from perpendicular. Sternite of 3rd pereopods with anterior lobe represented by single large capsulate seta. Sternites of 4th and 5th pereopods often with 1 to several capsulate setae. Fourth pereopod with propodal rasp consisting of several rows of corneous scales; dactyl moderately long, claw well developed; preungual process small to moderately well developed at base of claw.

Males and females both with paired gonopores; males without sexual tubes.

Abdomen straight or slightly flexed, usually moderately long. Uropods asymmetrical; exopods usually considerably larger than endopods. Telson without transverse suture; terminal margin entire, convex, unarmed. Males without paired pleopods, with 3 unpaired pleopods with endopods reduced or absent. Females

with paired 1st pleopods modified as gonopods, with 4 unpaired pleopods, 2nd–4th well developed and biramous, 5th moderately well developed, uniramous or weakly biramous.

Distribution.—Pacific Ocean: Southern California to Baja California, Mexico; Gulf of California, Mexico to Costa Rica; 20–275 m.

Etymology.—*Enallopaguropsis* is from the Greek *enallo* meaning changed, *pagouros*, a crab, and *opseo*, appearance, referring to the changed structural development of the telson from the typical pagurid type.

KEY TO THE SPECIES OF *ENALLOPAGUROPISIS*

- 1a. Dorsolateral margin of carpus of right cheliped unarmed; dorsal surface of palm and fixed finger with closely spaced granules armed with small corneous spinules *E. guatemoci*
- 1b. Dorsolateral margin of carpus of right cheliped armed with sparse row of spines; dorsal surface of palm and fixed finger with scattered unarmed tubercles *E. janetae* n. sp.

Enallopaguropsis guatemoci (Glassell, 1937)

Figures 9a, 10a–c

Pylopagurus guatemoci Glassell, 1937: 254 (type locality: 31°25'N, 116°42'W, Baja California, Mexico).—Walton, 1954: 146, pl. 43, Fig. B.—Gordan, 1956: 340.—Scanland and Hopkins, 1969: 259.

Pylopagurus hancocki Walton, 1954: 148, pl. 41 (type locality: off San Francisquito Bay, Gulf of California, Mexico, VELERO III station 534-36).—Gordan, 1956: 340.—Scanland and Hopkins, 1969: 260.

Enallopaguropsis guatemoci: McLaughlin, 1981a: 8 (by implication).

Holotype (*P. guatemoci*).—♂ (SL = 3.0 mm), New York Zool. Soc. 36801.

Holotype (*P. hancocki*).—♂ (SL = 1.8 mm), AHF 362.

Material Examined.—See Table 1.

Diagnosis.—Shield as long as or longer than broad; rostrum obtusely triangular, sometimes as small lobe, with or without terminal spine; lateral projections obtusely triangular or broadly rounded, with small marginal or submarginal spine. Ocular peduncles moderately long and stout, corneae slightly dilated; ocular acicles narrowly triangular or subovate, with strong submarginal spine; separated basally by approximate basal width of 1 acicle. Right cheliped with merus unarmed. Carpus with 1 or 2 strong spines on dorsomesial margin separated from stronger distal spine by broad, shallow depression, occasionally with few accessory spinules proximally and on dorsal surface. Palm with dorsomesial, proximal and dorsolateral margins each with row of strong spines, more irregular in larger animals; dorsal surface of palm and fixed finger with closely spaced, irregular granules often provided with corneous spinules or short spiniform bristles. Dactyl with row of strong, sometimes irregular spines on dorsomesial margin, dorsal surface somewhat elevated in midline and provided with numerous irregular granules frequently armed with corneous spinules. Left cheliped sometimes with small spine at ventrolateral distal angle of merus. Carpus with row of moderate to strong spines on dorsolateral margin, occasionally also strong spine on dorsodistal margin. Palm and fixed finger somewhat elevated in midline and armed with irregular row of small spines, strongest proximally, dorsal surface with scattered granules, dorsolateral margin with row of strong spines; dactyl unarmed but with tufts of long stiff setae, particularly ventrally. Dactyls of 2nd and 3rd pereopods short, broad; ventral margins and mesial faces dorsally each with row of corneous spines; propodi with few corneous spines on ventral margins distally. Sternite of 3rd

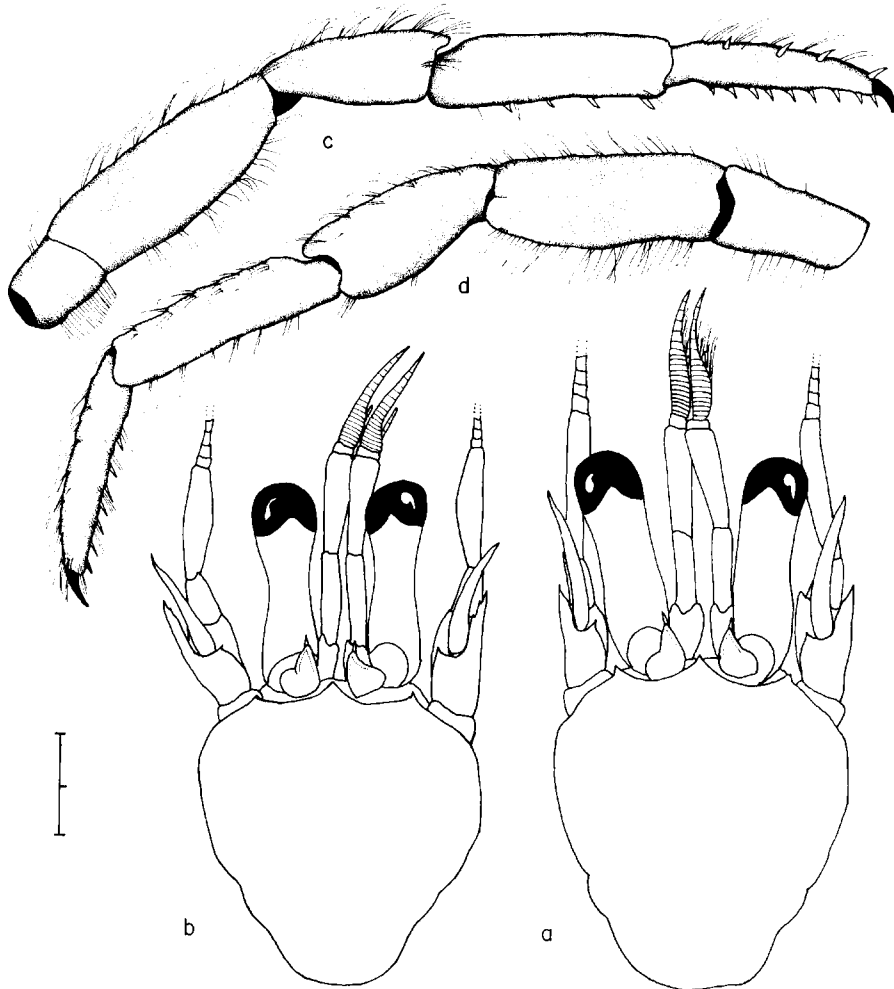


Figure 9. Shields, cephalic appendages and pereopods: (a) *Enallopaguropsis guatemoci*; (b–d) *Enallopaguropsis janetae* new species—(b) shield and cephalic appendages; (c) left 2nd pereopod (mesial view); (d) left 3rd pereopod (lateral view).

pereopods with anterior lobe replaced by very large capsulate setae. Sternites of 4th and 5th pereopods usually with 1 to several capsulate setae. Uropods somewhat asymmetrical. Telson without transverse suture; terminal margin entire, convex, unarmed.

Distribution.—Southern California to Baja California, Mexico; Gulf of California, Mexico; 20–275 m.

Remarks.—Walton (1954) described *Pylopagurus hancocki* as a species that could be distinguished from *E. guatemoci* because the former taxon had three spines on the dorsomesial margin of the carpus of the right cheliped, whereas the latter had only two. The only other distinguishing characters reported were a truncate rostrum and a partially cleft spine on the carpus of the left cheliped. As has been seen in species of *Enallopagurus* the number of proximal spines on the dor-

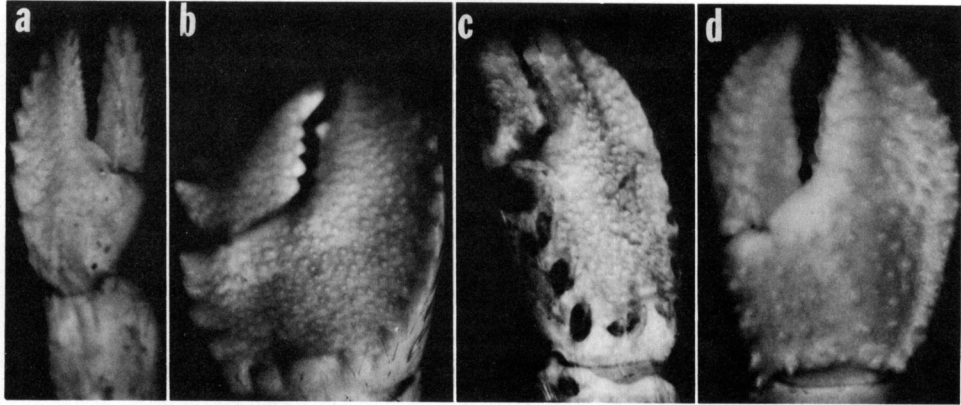


Figure 10. Left and right chelae: (a–c) *Enallopaguropsis guatemoci*—(a) left chela (20.6 \times); (b) right chela (19.8 \times); (c) right chela of *Pylopagurus hancocki* holotype (17.9 \times); (d) *Enallopaguropsis janetae* new species, right chela (12.4 \times).

somesial margin of the carpus of the right cheliped is subject to variation. Similarly, the shape of the rostrum is variable in many hermit crab taxa, and a bifid or cleft spine rarely can be considered diagnostic. Although the right chela is appreciably narrower in the single specimen known of *P. hancocki* than is typical of *E. guatemoci*, in this and all other characters, Walton's taxon is within the range of intraspecific variation that can be expected. Therefore, I believe that *P. hancocki* must be considered a junior subjective synonym of *E. guatemoci*.

Enallopaguropsis janetae new species

Figures 9b–d, 10d, 11

Holotype.—♀ (SL = 3.0 mm), AHF 725, type locality: 1.6 miles WNW of Punta Gissler, Cocos Island, SEARCHER station 521.

Material Examined.—See Table 1.

Description.—Shield longer than broad, anterior lateral margins sloping, anterior margins between rostrum and lateral projections slightly concave, posterior margin truncate; dorsal surface with few tufts of setae. Rostrum exceeding lateral projections, triangular, with median raised lobe, terminating in small spine. Lateral projections obtusely triangular with small submarginal spine.

Ocular peduncles moderately long, broadened somewhat basally and with corneae slightly dilated; dorsal and mesial faces with few scattered setae. Ocular acicles narrowly triangular, dorsal surface somewhat concave, with strong submarginal spine; separated basally by approximate basal width of 1 acicle.

Antennular peduncles moderately long, exceeding ocular peduncles by one-half length of ultimate segment. Ultimate and penultimate segments with scattered setae; basal segment with strong spine on lateral face medially.

Antennal peduncles moderately short, only slightly exceeding length of ocular peduncles; with supernumerary segmentation. Fifth, fourth, and third segments unarmed. Second segment with dorsolateral distal angle produced, terminating in strong spine, mesial margin with 1 or 2 acute spines, lateral margin unarmed; dorsomesial distal angle with small spine, mesial margin with few setae. First segment with ventral margin produced anteriorly and terminating in strong acute spine. Antennal acicle somewhat arcuate, terminating in small spine, and with

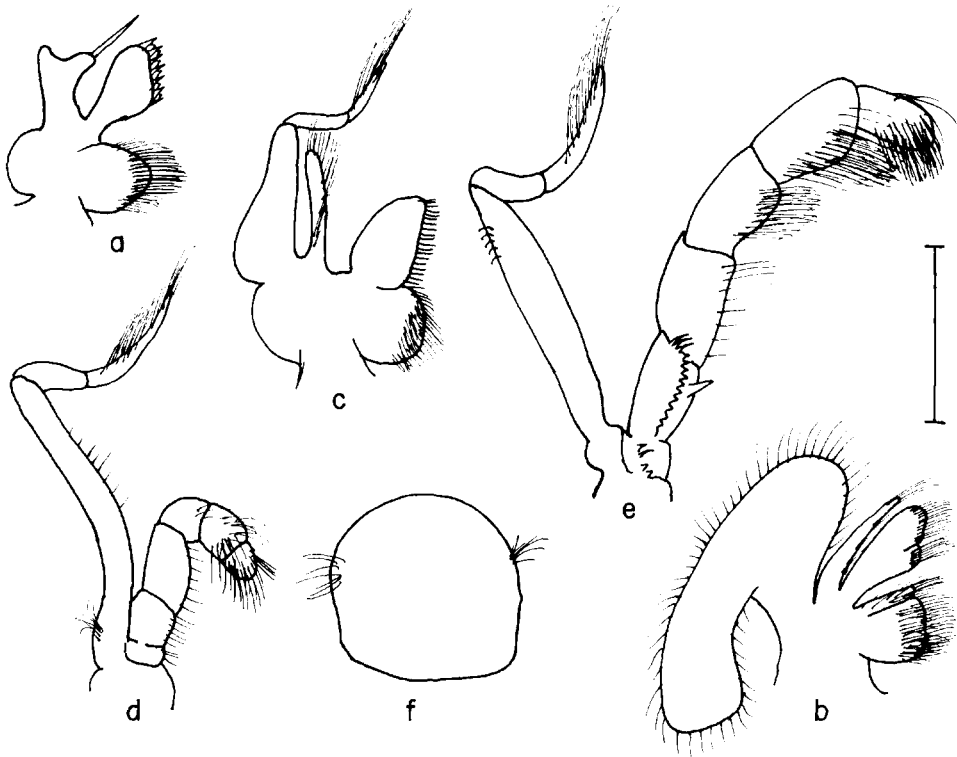


Figure 11. *Enallopaguropsis janetae* new species: a–e, mouthparts (left, internal view)—(a) maxillule; (b) maxilla; (c) 1st maxilliped; (d) 2nd maxilliped; (e) 3rd maxilliped; (f) telson. Scale equals 1 mm.

numerous tufts of setae. Antennal flagella with long (3–4 articles in length) and short setae every 2nd or 3rd article.

Mandible without distinguishing characters. Maxillule (Fig. 11a) with 1 stiff bristle on moderately well developed internal endopodal lobe, external lobe moderately well developed; proximal endite generally subcircular. Maxilla (Fig. 11b) with endopod approximately equalling scaphognathite in distal extension. First maxilliped (Fig. 11c) with basal segment of exopod slender. Second maxilliped (Fig. 11d) without distinguishing characters. Third maxilliped (Fig. 11e) with well developed crista dentata and accessory tooth, merus with dorsodistal spine. Sternite of 3rd maxillipeds with spine on either side of midline.

Right cheliped with dactyl exceeding length of palm, moderately broad; cutting edge with row of calcareous teeth, terminating in minute corneous claw; overlapped by fixed finger; dorsal surface slightly elevated in midline and armed with scattered small spines; dorsomesial margin with row of irregularly sized, blunt spines; ventral and mesial faces with scattered low protuberances and few short to moderately long setae. Palm slightly shorter than carpus; dorsal surface of palm and fixed finger with scattered tubercles, strongest proximally; dorsomesial and dorsolateral margins each with moderately strong or strong spines; ventral, mesial and lateral surfaces with low, sometimes spinulose protuberances and scattered tufts of setae; cutting edge of fixed finger with row of calcareous teeth, terminating in small corneous claw. Carpus approximately equalling merus in

length; dorsomesial margin with 2 prominent spines separated by broad, shallow depression, dorsal surface with proximal row of low protuberances laterad of midline, becoming small spines distally; ventral, lateral, and mesial faces with scattered setae. Merus subtriangular, unarmed. Ischium unarmed. Coxa with tuft of stiff bristles at ventromesial distal angle.

Left cheliped missing.

Ambulatory legs moderately long, slightly overreaching right cheliped. Right 2nd pereopod missing, left and 3rd pair similar. Dactyls approximately equalling length of propodi, moderately broad; in dorsal and lateral views, generally straight; terminating in moderately long, slightly curved claws; dorsal surfaces with few tufts of fine setae; ventral margins and mesial faces dorsally each with row of strong corneous spines; lateral faces with scattered setae. Propodi slightly longer than carpi; dorsal margins with tufts of moderately long setae; ventral margins each with row of corneous spines, at least in distal half. Carpi somewhat shorter than meri; dorsal surfaces each with row of tufts of fine setae; ventral margins with scattered setae. Meri laterally compressed; dorsal and ventral margins with tufts of setae. Ischia with tufts of setae on dorsal and ventral margins. Coxae and bases distinct, each with few fine setae. Sternite of 3rd pereopods with anterior lobe represented by large capsulate seta. Sternite of 4th pereopod with slender capsulate seta. Fourth pereopods with propodal rasp consisting of five rows of corneous scales; claw of dactyl stout, preungual process moderately small.

Fifth pleopod of female not appreciably reduced in size but uniramous. Male unknown. Uropods somewhat asymmetrical; protopods each with small spine-like projection; exopods each with ventral row of long, moderately stiff setae. Telson without transverse suture; terminal margin entire, convex, unarmed.

Distribution.—Known only from the type locality.

Remarks.—*E. janetae*, although known only from the female holotype, is clearly related to the other species assigned to *Enallopaguropsis*. It may be distinguished from that species by its tuberculate armature of the right chela, and by the lack of strong spines on the proximal margin of the palm.

This species is named for the eminent carcinologist, Janet Haig, who has contributed so much to our knowledge of Pacific hermit crabs, and who made this species available to me.

INTERSPECIFIC RELATIONSHIPS

The eight species assigned to *Agaricochirus* are known from relatively few specimens; therefore, interspecific relationships have been difficult to assess. Each species has evolved its own distinctive armature and ornamentation of the chelae, although *A. boletifer* and *A. alexandri* are, at least superficially, quite similar and presumably closely related. Three species, *A. hispidus*, *A. gibbosimanus*, and *A. echinatus* must be considered closely allied species, despite the great diversity in the structure and ornamentation of their respective chelae. In these species the fifth abdominal tergite, and often also the fourth and third, is delineated by patches of stiff setae. Not uncommonly these tergites also may be reinforced with chitin or weakly calcified. Such demarcation of abdominal tergites is extremely rare among species of the Paguridae, thus it seems improbable that this condition would have evolved independently in three species of a single genus. The relationships of *A. erosus* and *A. acanthinus* with other members of the genus are not clear, but presumably both are more closely related to *A. boletifer* and *A. alexandri* than to members of the *A. hispidus* group. *A. cavi-manus* is known from only two female specimens; however, the extremely vaulted

carapace, markedly concave right chela, and more slender ocular acicles suggest that this species is only distantly related to other members of the genus.

Morphological evidence suggests that species of *Enallopagurus* and *Enallopaguroopsis* all are closely related. Major distinguishing characters are the structure of the anterior lobe of the sternite of the third pereopods and the development of the propodal rasp of the fourth pereopods. The uropods of *Enallopagurus* species may be symmetrical or asymmetrical, but those of *Enallopaguroopsis* are asymmetrical. Species of both genera share the distinctive armature of the carpus of the right cheliped, which consists of 2 to 4 widely spaced spines on the dorso-mesial margin, the distal-most spine often separated from the others by a broad concavity. With the exception of one other small Pacific genus, *Discorsopagurus*, the structure of the telson sets these genera apart from all other genera of the Paguridae; however, the terminal margin is armed in *Discorsopagurus* and unarmed in both *Enallopagurus* and *Enallopaguroopsis*. In discussing the structure of the telson in *Discorsopagurus* (McLaughlin, 1974), I suggested that it might indicate a relationship with species of the Parapaguridae. In view of the numerous other morphological differences in parapagurids, any relationship that might have existed, would have to have occurred between sister groups that diverged quite early in the evolutionary history of paguroids. The lack of a well defined transverse suture in the telsons of some species of *Agaricochirus* is not homologous with the conditions in *Enallopagurus*, *Enallopaguroopsis*, or the Parapaguridae.

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