

***Pteropagurus* and *Catapagurus* (Decapoda, Anomura, Paguridae): resource sharing or “any port in a storm”?**

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ABSTRACT

Additional materials of two species of the recently described pagurid genus *Pteropagurus* McLaughlin & Rahayu, 2006 have required an emendation of the genus. These have also provided the information needed to supplement the original species descriptions, including the unusual morphology of the male of *P. spina* McLaughlin & Rahayu, 2006 and the sexual dimorphism and variability found in *P. spinulocarpus* McLaughlin, 2007. Brief data on the larval development in *Pteropagurus* have been gleaned from zoeae prematurely hatched from one female of *P. spinulocarpus*. What heretofore had been considered a unique habitat for species of this genus, i.e. empty shells of a pelagic pteropod, was found to also provide carcinoecia for *Catapagurus spinicarpus* de Saint Laurent & McLaughlin, 2000, a species previously known only from its female holotype collected in the Kermadec Islands of New Zealand. The male of this species is described and species' variability and dimorphic attributes are assessed. Consideration is given to the question of habitat choice and the morphological adaptations required for use of the unusual carcinoecia.

KEY WORDS

Crustacea,
Decapoda,
Anomura,
Paguridae,
Pteropagurus,
Catapagurus,
Cuvierina,
larval attributes,
pteropod shells,
resource sharing.

Pteropagurus et *Catapagurus* (Decapoda, Anomura, Paguridae): partage de ressources ou « nécessité fait loi »?

L'examen de nouveaux spécimens du genre récemment décrit *Pteropagurus* McLaughlin & Rahayu, 2006 entraîne une émendation du genre. Ces spécimens ont aussi apporté des informations permettant de compléter les descriptions originales des espèces, incluant la morphologie inhabituelle du mâle de *P. spina* McLaughlin & Rahayu, 2006 et le dimorphisme sexuel et la variabilité trouvés chez *P. spinulocarpus* McLaughlin, 2007. Des données sur le développement larvaire de *Pteropagurus* ont été fournies par les zoés prématurément écloses d'une femelle de *P. spinulocarpus*. Ce qui était considéré jusqu'à présent comme l'habitat exclusif des espèces du genre, c'est-à-dire des coquilles vides de ptéropodes pélagiques, s'avère aussi fournir des carcinoecia pour *Catapagurus spinicarpus* de Saint Laurent & McLaughlin, 2000, une espèce qui n'était connue que par l'holotype femelle récolté aux îles Kermadec en Nouvelle-Zélande. Le mâle de cette espèce est décrit, la variabilité spécifique et les attributs dimorphiques sont établis. Le choix de l'habitat et les adaptations morphologiques nécessaires pour l'utilisation d'un carcinoecium inhabituel sont discutés.

MOTS CLÉS

Crustacea,
Decapoda,
Anomura,
Paguridae,
Pteropagurus,
Catapagurus,
Cuvierina,
attributs larvaires,
coquilles de ptéropodes,
partage des ressources.

INTRODUCTION

McLaughlin & Rahayu (2006) described a new genus and two new species of hermit crabs whose morphological adaptations to a unique habitat appeared to set them apart from all other hermit crabs. That habitat was shells of a pelagic mollusc, a member of the order Thecosomata Blainville, 1824, commonly referred to as pteropods. The hermit crab genus was appropriately named *Pteropagurus* McLaughlin & Rahayu, 2006. The species, *Pteropagurus spina* McLaughlin & Rahayu, 2006 and *P. inermis* McLaughlin & Rahayu, 2006, were described from one and six individuals, respectively. A third species, *P. spinulocarpus* McLaughlin, 2007 was subsequently described, but again from a paucity of material – only five specimens. Interestingly, one of the localities where *P. spinulocarpus* was collected was also the type locality for *P. spina*, suggesting that the two species might occur sympatrically.

A station very near that earlier site in the Chesterfield Islands of the New Caledonia Economic Zone was revisited during the EBISCO cruise of 2005. On this latter occasion, 34 specimens

of *P. spinulocarpus* and a solitary male of *P. spina* were collected. However, the sample provided much more than supplemental information on these poorly known species. Additionally, empty pteropod shells were occupied, not only by the two *Pteropagurus* species, but unexpectedly also by a species of the genus *Catapagurus* A. Milne-Edwards, 1880. *Catapagurus spinicarpus* de Saint Laurent & McLaughlin, 2000, at the time thought to be an endemic New Zealand taxon, had been known only from its female holotype.

Knowledge of the male of *P. spina* not only broadens our assessment of the intrageneric variability occurring within *Pteropagurus*, but requires further emendation to the generic diagnosis. Larvae from one ovigerous female of *P. spinulocarpus* hatched prematurely at the time of preservation, and while the specimens were not sufficiently well developed to allow a detailed description of the first zoeal stage, it was possible to determine that despite the moderately large size and relatively small number of eggs carried by females of this species, the first zoeal stage was typical of pagurid larvae. The supplemental specimens of both *P. spinulocarpus* and *C. spinicarpus* now permit amendments

to the original descriptions that include information on growth related morphological changes, sexual dimorphism and adaptations to pteropod carcinoecia.

MATERIAL AND METHODS

With the exception of the holotype of *C. spinicarpus* deposited in the National Museum of New Zealand (now Museum of New Zealand Te Papa Tongarewa), Wellington (NMNZ), the materials reported herein are deposited in the collections of the Muséum national d'Histoire naturelle, Paris (MNHN) with the catalog code Pg. MUSORSTOM is the acronym for the joint expeditions of the MNHN and the Office de la Recherche scientifique et technique d'Outre-Mer (ORSTOM), now Institut de Recherche pour le Développement (IRD); EBISCO is the acronym for Exploration de la Biodiversité et ISolement en Mer du COrail. Specific collection gear used precedes the station number; gear abbreviations are: CC, otter trawl (shrimp); DC, Charcot dredge; DW, Warén dredge; BS refers to benthic sample. Latitudes and longitudes are given only for the start of each gear deployment. One measurement, shield length, measured from the tip of the rostrum or midpoint of the rostral lobe to the midpoint of the posterior margin of the shield, and rounded to the nearest 0.1 mm, is given in parentheses following the specimen sex and provides an indication of animal size. It must be pointed out that shield width, more than length, increases with increasing animal size in *P. spinicarpus* as it does in most species of *Catapagurus* (McLaughlin personal observation); however, shield contours make precise measurements of width unreliable. Ocular peduncle length was measured on the lateral surface of the left peduncle from the distal margin of the cornea to the proximal margin of the ultimate peduncular segment; corneal diameter represented the maximum diameter of the cornea measured across the dorsal surface. Selected specimens and larvae were stained with Chlorzale Black E to enhance observations. Abbreviations used in the text are stn and ovig. for station and ovigerous, respectively.

SYSTEMATICS

Family PAGURIDAE Latreille, 1802

Genus *Pteropagurus*

McLaughlin & Rahayu, 2006 emended

Pteropagurus McLaughlin & Rahayu, 2006: 56. — McLaughlin 2007: 504.

TYPE SPECIES. — *Pteropagurus inermis* McLaughlin & Rahayu, 2006 by original designation.

EMENDED DIAGNOSIS. — Eleven pairs of biserial phyllobranchiate gills. Rostrum triangular, broadly rounded or obsolete; lateral projections well developed or obsolete. Ocular peduncles moderate to stout, corneas prominently dilated or not; ocular acicles triangular, each often with marginal or submarginal terminal spine. Antennal peduncles with supernumerary segmentation. Mandible with entirely calcified cutting edge. Maxillule with external lobe of endopod obsolete, internal lobe with 1 stiff seta. Maxilla with endopod reaching to or considerably overreaching distal margin of scaphognathite. First maxilliped with slender exopod. Second maxilliped without distinguishing characters. Third maxilliped with crista dentata reduced, no accessory tooth. Sternite of third maxillipeds (thoracic somite IX of Pilgrim 1973) unarmed. Sternite of chelipeds (thoracic somite X) quite narrow, incompletely fused to much broader sternite of second pereopods. Sternite of third pereopods (thoracic somite XII) sexually dimorphic or not: varying from only slightly broadened and not produced posteriorly to broad and prominently produced posteriorly.

Chelipeds long, slender, right appreciably stouter, but not always longer. Second pereopods somewhat or markedly shorter than third; dactyls with or without ventral corneous spines. Fourth pereopods semichelate or weakly subchelate, propodal rasps with few scales; no preungual process. Fifth pereopods chelate, rasps moderately well developed.

Males with elongate, stout right or left sexual tube directed posteriorly and externally and curving up over anterior portion of pleon; alternate coxa with or without papilla or short tube; left pleopods 3 and 4 uniramous or unequally biramous; pleopod 5 uniramous. Females with paired gonopores or unpaired left; no paired and modified first pleopods, unpaired biramous left pleopods 2-4, pleopod 5 uniramous as in males. Pleon somewhat reduced, straight; pleomere 1 partially fused with last thoracic somite, tergites 2-5 weakly delineated or not; tergite 6 chitinous. Uropods symmetrical; protopods each with or without posteriorly directed spine; exopods elongate, endopods reduced, both with 1 or 2 marginal rows of scales. Telson without transverse incisions, with

slight to moderately well developed median cleft or concavity; terminal margins rounded or oblique, unarmed, with few minute bristles, very small tubercles, or tiny spines.

REMARKS

In proposing their new genus *Pteropagurus*, McLaughlin & Rahayu (2006) noted certain morphological attributes of the two assigned species, *P. inermis* and *P. spina* that they considered adaptations to the cylindrical pteropod shells that served as carcinoecia. These included the reduced and straight, albeit somewhat swollen pleons, the distinctly elongate third pereopods, the broadened and posteriorly lengthened sternite of the third pereopods, and the carriage of the uropods and telson that were routinely folded under the pleon. However, their interpretations were based on data gleaned primarily from *P. inermis*, for which both males and females were available for examination. The broadening of sternite XII (sternite of the third pereopods) occurred in males of *P. inermis*, but not in females of either species and therefore was considered a sexually dimorphic character of the genus. When *P. spinulocarpus* was recognized, McLaughlin (2007) found that the broadening and elongation of this sternite occurred in both sexes. Now, with the discovery of a male of *P. spina*, elongation of the sternite of the third pereopods can no longer be viewed as a direct adaptation to the pteropod carcinoecium. Neither male nor female of this species exhibit any unusual lengthening of the sternite. McLaughlin & Rahayu (2006) suggested that the dimorphic sternal elongation might be correlated to an increase in the breadth of the cephalothorax in males of *P. inermis*. However, with the information currently available for all three species, another hypothesis appears more feasible. The third pereopods are longer than the second in both males and females of all three species, but markedly so only in males of *P. inermis* and both sexes of *P. spinulocarpus* where the sternite is also lengthened. In contrast, females of *P. inermis* and both male and female of *P. spina* lack the pronounced elongation of the sternite of the third pereopods and of the third pereopods themselves. Thus it may be that the posterior development of the sternite of

the third pereopods is in response to the exceptional development of this third pair of appendages.

Development of the sexual tube in *P. spina* presents a more serious dilemma for emendation of the generic diagnosis. Males of both *P. inermis* and *P. spinulocarpus* are characterized by an elongate sexual tube developed from the coxa of the right fifth pereopod that is directed toward the exterior and curves up over the dorsal surface of the pleon on the right side of the body. The sexual tube of the just discovered male of *P. spina* develops from the coxa of the left fifth pereopod, is directed toward the exterior and curves up and over the dorsal surface of the pleon from left to right, and extends almost to the gonopore of the right coxa on the ventral body surface. This disparity in sexual tube development could easily be considered justification for the establishment of a second genus of pteropod-dwelling hermit crabs. Additionally, the moderately slender ocular peduncles and corneas lacking appreciable dilation, together with the development of a prominent rostrum only in *P. spina* tends to support such a distinction. However, as McLaughlin & Rahayu (2006) emphasized, *P. inermis* and *P. spina* share several synapomorphies and these are similarly shared with *P. spinulocarpus*. Additionally, the magnitude of differences in lengths of the second and third pereopods and the elongation of the sternite of the third pereopods appear to be clinal, with *P. spina* being the least, *P. spinulocarpus* the most advanced, with *P. inermis* intermediate and dimorphic. With only one male of *P. spina* yet known, it is not possible to determine with certainty that the left sexual tube development in this species is typical or represents an abnormality. Clearly, there is no abnormal development in the tube itself other than its unusual length. However, one of the authors (PMcL) has observed the atypical development of the right sexual tube in two specimens of *Catapagurus franklinae* McLaughlin, 2004, where the tube is directed from right to left across the ventral body surface as it is in species of *Cestopagurus* Bouvier, 1897. Consequently, we believe that it is more appropriate to consider sexual tube development in *Pteropagurus* species variable, until such time as additional data prove the contrary.

Pteropagurus spina

McLaughlin & Rahayu, 2006

(Fig. 1)

Pteropagurus spina McLaughlin & Rahayu, 2006: 64, fig. 5. — McLaughlin 2007: 508.

HOLOTYPE. — New Caledonia. MUSORSTOM 5, stn DW 274, 24°44.8'S, 159°41.0'E, 285 m, 9.X.1986, ovig. ♀ (1.2 mm) (MNHN-Pg 7637).

NEW MATERIAL EXAMINED. — New Caledonia. EBISCO, stn DW 2492, 24°44.0'S, 159°41.0'E, 285 m, 6.X.2005, 1 ♂ (1.3 mm) (MNHN-Pg 7763).

DISTRIBUTION. — Presently known only from the type locality, Chesterfield Plateau, and vicinity, New Caledonia; 285 m.

DESCRIPTION OF MALE

Shield (Fig. 1A) slightly broader than long, weakly calcified; anterior margin between rostrum and lateral projections concave; anterolateral margins sloping; posterior margin roundly truncate. Triangular rostrum produced slightly beyond midlength of ocular acicles; lateral projections each with acute marginal spine. Carapace lateral lobes reaching 0.4 of shield. Posterior carapace with moderately narrow median plate; cardiac sulci reaching to posterior margin. Branchiostegites membranous, unarmed.

Ocular peduncles moderately stout but not noticeably broadened distally, 0.7 length of shield; corneal diameter 0.5 of total peduncular length; ocular acicles narrowly triangular, reaching to or beyond proximal margin of ultimate peduncular segment, each with moderately large submarginal spine.

Antennular peduncles overreaching distal margins of corneas by slightly less than lengths of ultimate peduncular segments; ultimate segment with 1 long, stiff seta on dorsodistal margin; penultimate segment with very few scattered setae; basal segment with acute spine on dorsolateral margin, ventral margin not produced distally.

Antennal peduncles overreaching distal corneal margins by 0.5 lengths of ultimate segments. Fifth and fourth segments with very few scattered setae; third segment with small spine at ventrodistal angle; second segment with dorsolateral distal angle produced, terminating in small spine, dorsomesial

angle with prominent spine; first segment with spine at dorsolateral distal margin, ventrolateral margin unarmed. Antennal acicle reaching beyond distal margin of fourth peduncular segment, moderately slender, terminating in simple spine. Antennal flagellum with 1 or 2 very short to moderately long setae every article.

Chelipeds subequal in length, but right slightly stouter; dactyls and fixed fingers each with small hiatus. Right cheliped (Fig. 1B) with dactyl equal to length of palm; dorsomesial margin smooth, dorsal surface somewhat convex, unarmed, but with few scattered, short setae mesially and ventrally; cutting edge with 2 low, broad, calcareous teeth, terminating in tiny corneous claw, slightly overlapped by fixed finger. Palm longer than carpus, dorsomesial margin delimited by 3 widely-spaced, acute spines and sparse tufts of setae, dorsal surface weakly convex, unarmed; dorsal surface of fixed finger similarly unarmed, dorsolateral margin smooth and with few scattered short setae; cutting edge with 3 broad, low calcareous teeth, terminating in tiny corneous claw. Carpus approximately equal to length of merus; dorsomesial distal angle with acute spine and 1 additional small spine on dorsomesial margin, dorsal surface with 2 small spines in lateral 0.3, dorsolateral margin not distinctly delimited; remaining surfaces unarmed. Merus with all surfaces unarmed; ventromesial and ventrolateral margins each with small spine at distal angle. Ischium unarmed.

Left cheliped (Fig. 1C) approximately equal to length of right, slightly slenderer. Dactyl equal to length of palm; surfaces rounded and unarmed, but with sparsely scattered, moderately long setae ventrally; cutting edge with row of minute calcareous teeth, terminating in small corneous claw. Palm with convex dorsal surface unarmed but with few scattered setae; dorsomesial margin with 3 small spines, dorsolateral margin not delimited; fixed finger rounded and unarmed but with several moderately long setae laterally; cutting edge with row of minute calcareous teeth, terminating in small corneous claw. Carpus equal to length of palm; dorsomesial margin not distinctly delimited but with acute spine at distal angle, without small spine at midlength, dorsal surface with 2 small spines laterad of midline,

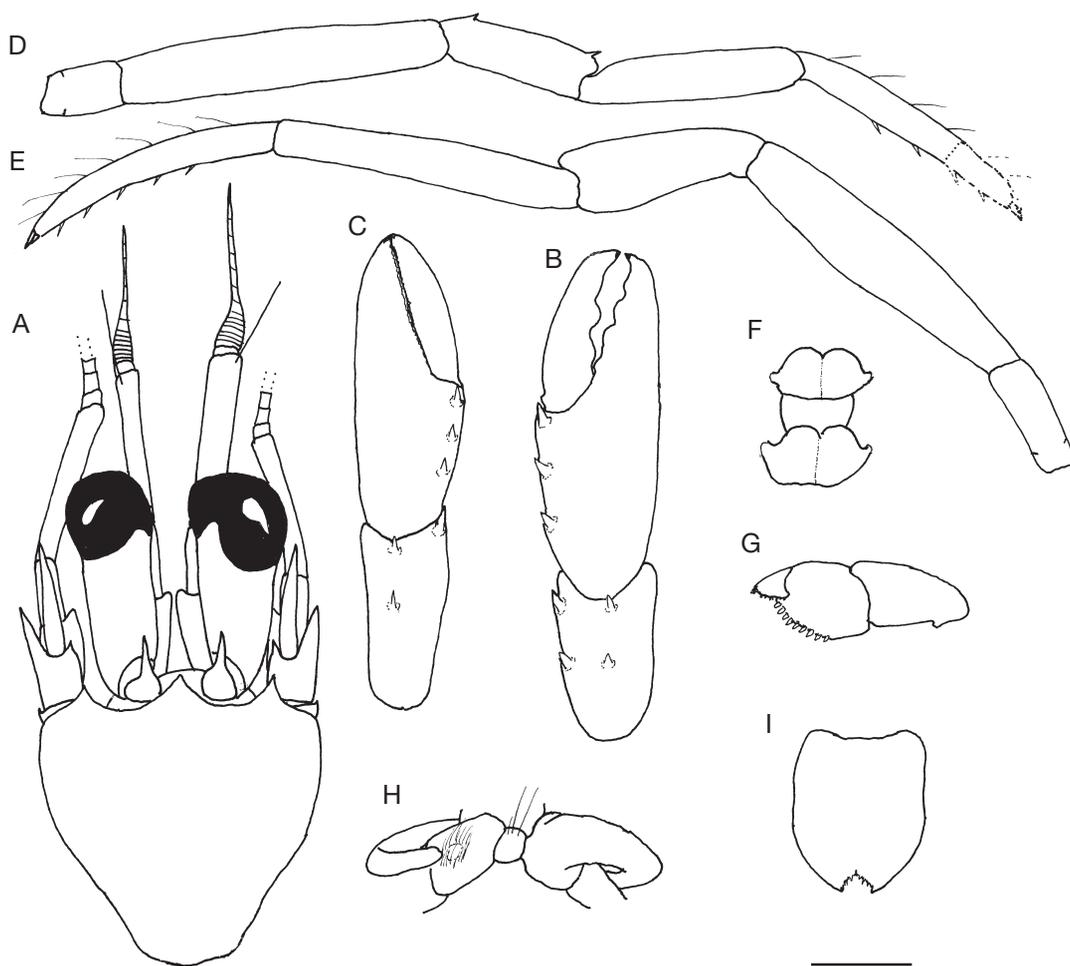


FIG. 1. — *Pteropagurus spina* McLaughlin & Rahayu, 2006, ♂ (1.3 mm), EBISCO, stn DW 2492, New Caledonia (MNHN-Pg 7763): **A**, shield and cephalic appendages, dorsal view (aesthetascs and most setae omitted); **B**, carpus and chela of right cheliped, dorsal view (setae omitted); **C**, carpus and chela of left cheliped, dorsal view (setae omitted); **D**, right second pereopod, lateral view (setae shown for dactyl only); **E**, left third pereopod, lateral view (setae shown for dactyl only); **F**, sternites of second and third pereopods, ventral view (setae omitted); **G**, distal three segments of left fourth pereopod, lateral view (setae omitted); **H**, coxae and sternite of fifth pereopods, ventral view; **I**, telson, dorsal view. Scale bar: A-F, H, 0.5 mm; G, I, 0.25 mm.

dorsolateral margin not delimited; remaining surfaces unarmed but with few scattered setae, ventromesial distal angle with small spine. Merus with surfaces unarmed but with few scattered short setae, ventromesial and ventrolateral distal angles each with small spine. Ischium unarmed.

Second and third pereopods (Fig. 1D, E) similar in armature but unequal in length, second shorter. Dactyls relatively straight in dorsal and lateral views,

slightly shorter to slightly longer than propodi, dorsal surfaces each with row of widely-spaced setae; ventral surfaces each with 4 or 5 corneous spines and few setae. Propodi slightly to considerably longer than carpi; surfaces all unarmed but with sparse setae dorsally and ventrally. Carpi of second pereopods each with dorsodistal spine and 1 additional spine on dorsal surface in proximal 0.5; carpi of third each without minute spinule at

dorsodistal margin, other surfaces unarmed but all with sparse setae. Meri unarmed, but each with few widely-spaced setae dorsally. Ischia unarmed. Sternite of third pereopods (Fig. 1F) not produced posteriorly. Fourth pereopods semichelate; propodal rasp (Fig. 1G) with 1 row of scales.

Extremely long sexual tube developed from coxa of left fifth pereopod (Fig. 1H), directed toward exterior, curved up and over dorsal surface of pleon and ventrally to level of coxa of right fifth pereopod; right coxa with gonopore circumscribed by moderately long, stiff setae.

Uropods symmetrical, each with 2 rows of scales on endopod and exopod. Telson (Fig. 1I) with posterior lobes separated by shallow median cleft, oblique terminal margins each with 3 or 4 very small spines, largest at apex.

Coloration

Not known.

Habitat

Empty shells of *Cuvierina columnella* (Rang, 1827).

REMARKS

Because of the paucity of material, the mouthparts of *P. spina* have not been removed for description and illustration, but appear to be in general agreement with those illustrated by McLaughlin & Rahayu (2006) for *P. inermis*, including the several teeth on the crista dentata of the third maxilliped. The general morphology of the male of *P. spina* differs only slightly from the female in proportions and spination of the chelipeds and ambulatory legs. However, the scales of the propodal rasp of the fourth pereopod form only a single row in this male. Having only one specimen of each sex, it is not possible to determine whether the two rows of spines in the female reflect a sexually dimorphic character or simply variation.

Pteropagurus spinulocarpus McLaughlin, 2007
(Figs 2; 3)

Pteropagurus spinulocarpus McLaughlin, 2007: 505, fig. 1.

HOLOTYPE. — **New Caledonia**. BIOCAL, stn DW 44, 22°47.30'S, 167°14.30'E, 440-450 m, 30.VIII.1985, ♂ (1.6 mm, posterior portion of pleon, uropods and telson missing) (MNHN-Pg 7738).

PARATYPES. — **New Caledonia**. MUSORSTOM 4, stn CC 212, 22°47.40'S, 167°10.50'E, 375-380 m, 28.IX.1985, 1 ovig. ♀ (1.5 mm, right cheliped and right second pereopod missing, left third pereopod regenerating) (MNHN-Pg 7737). — Stn DW 222, 22°57.60'S, 167°33'E, 410-440 m, 30.IX.1985, 1 ♀ (1.5 mm, with rhizocephalan, missing both chelipeds, left second and third right pereopods) (MNHN-Pg 7701).

MUSORSTOM 5, stn DW 274, 24°44.84'S, 159°41.00'E, 285 m, 9.X.1986, 1 ♀ (1.2 mm, missing right cheliped and both third pereopods) (MNHN-Pg 7702). — Stn DC 361, 19°52.50'S, 158°38.10'E, 400 m, 19.X.1986, 1 ♂ (1.5 mm, right cheliped regenerating; left cheliped with fixed finger broken off; left third pereopod missing) (MNHN-Pg 7700).

NEW MATERIAL EXAMINED. — **New Caledonia**. EBISCO, stn DW 2492, 24°44.0'S, 159°41.0'E, 285 m, 6.X.2005, 12 ♂♂ (1.2-1.7 mm, 1 with rhizocephalan), 7 ♀♀ (1.4-1.7 mm), 15 ovig. ♀♀ (1.4-1.6 mm) (MNHN-Pg 7764).

DISTRIBUTION. — **New Caledonia** from the Chesterfield Plateau to south of the Isle of Pines; 285-440, possibly 450 m.

SUPPLEMENTAL DESCRIPTION

Shield (Fig. 2A) with rostral lobe slightly to moderately produced, very faintly rounded to broadly and bluntly triangular, unarmed; lateral projections obsolete to roundly triangular, unarmed or with tiny marginal spinule. Ocular peduncles short and stout, appreciably broadened distally; ocular acicles narrowly to ovately triangular, slightly less to slightly more than 0.5 peduncular lengths; each terminating acutely or with prominent terminal spine. Antennular peduncles overreaching distal margins of corneas by 0.2-0.5 lengths of penultimate peduncular segments. Ultimate segment with 1-5 long setae at dorsodistal margin. Antennal peduncles overreaching distal corneal margins by 0.3-0.5 lengths of ultimate segments; second segment with dorsolateral distal angle produced, with acute terminal spine and often 1, occasionally 2, smaller spines on lateral margin subterminally; first segment with small to prominent spine on laterodistal margin; antennal acicle moderately

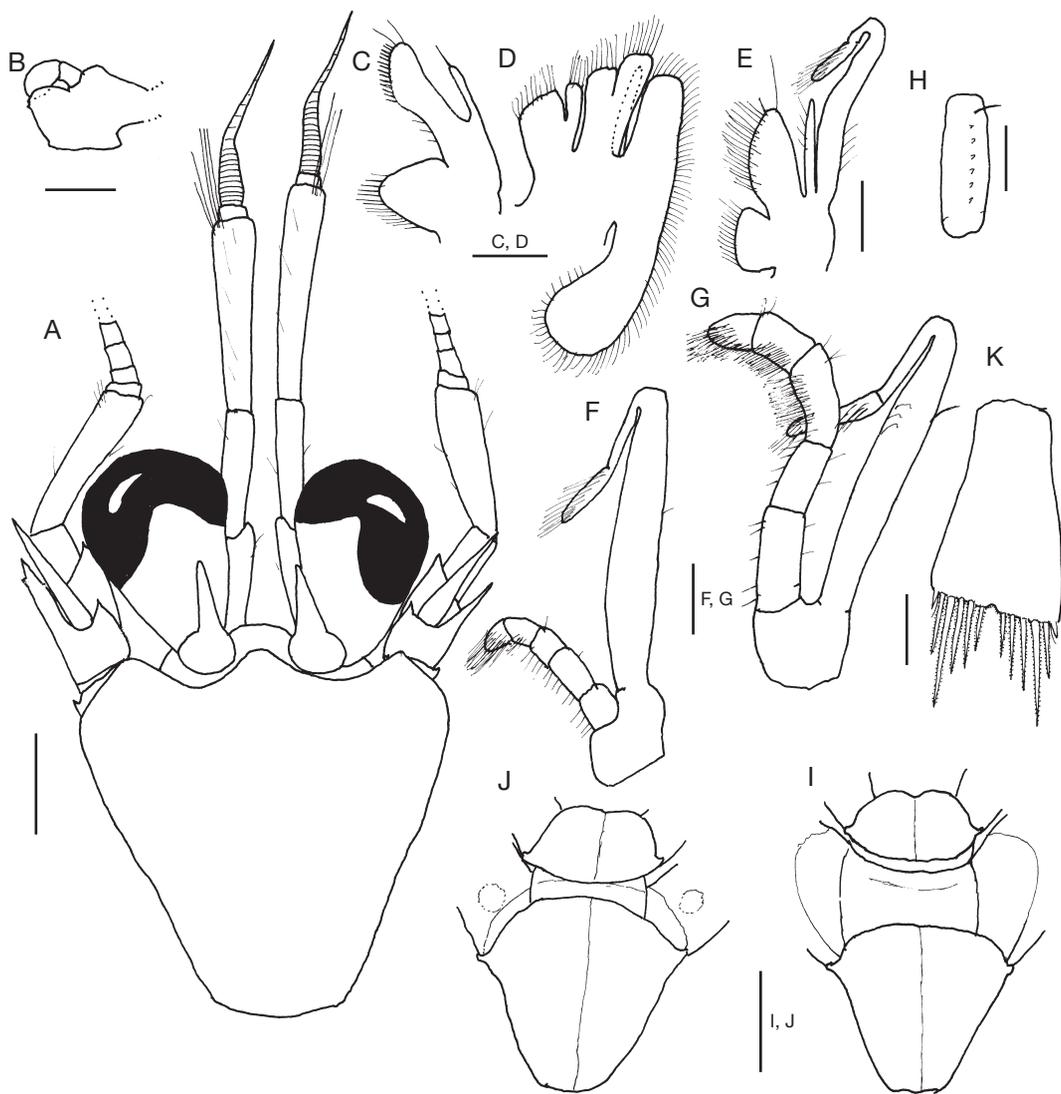


FIG. 2. — *Pteropagurus spinulocarpus* McLaughlin, 2007 from EBISCO, stn DW 2492, New Caledonia (MNHN-Pg 7764): **A**, shield and cephalic appendages, dorsal view (aesthetascs omitted); **B**, left mandible, outer view; **C**, left maxillule, outer view; **D**, left maxilla, outer view; **E**, left first maxilliped, outer view; **F**, left second maxilliped, outer view; **G**, left third maxilliped, outer view; **H**, ischium of left third maxilliped, inner view; **I, J**, sternites of second and third pereopods, ventral view; **K**, zoeal telson, dorsal view; **A, I, J**, ♂ (1.6 mm); **B-H**, ♂ (1.7 mm); **J**, ♀ (1.7 mm); **K**, zoea. Scale bars: A-J, 0.5 mm; K, 0.25 mm.

slender, reaching to or beyond distal margin of fourth peduncular segment.

Mandible (Fig. 2B) with 2-segmented palp. Maxillule (Fig. 2C) with external lobe of endopod obsolete, internal lobe with 1 seta; basal endite with very slender tooth-like marginal processes.

Maxilla (Fig. 2D) with endopod slightly overreaching distal margin of scaphognathite. First maxilliped (Fig. 2E) with endopod overreaching basal endite; slender exopod with few marginal setae. Second maxilliped (Fig. 2F) with very long exopod. Third maxilliped (Fig. 2G) with basis-ischium almost

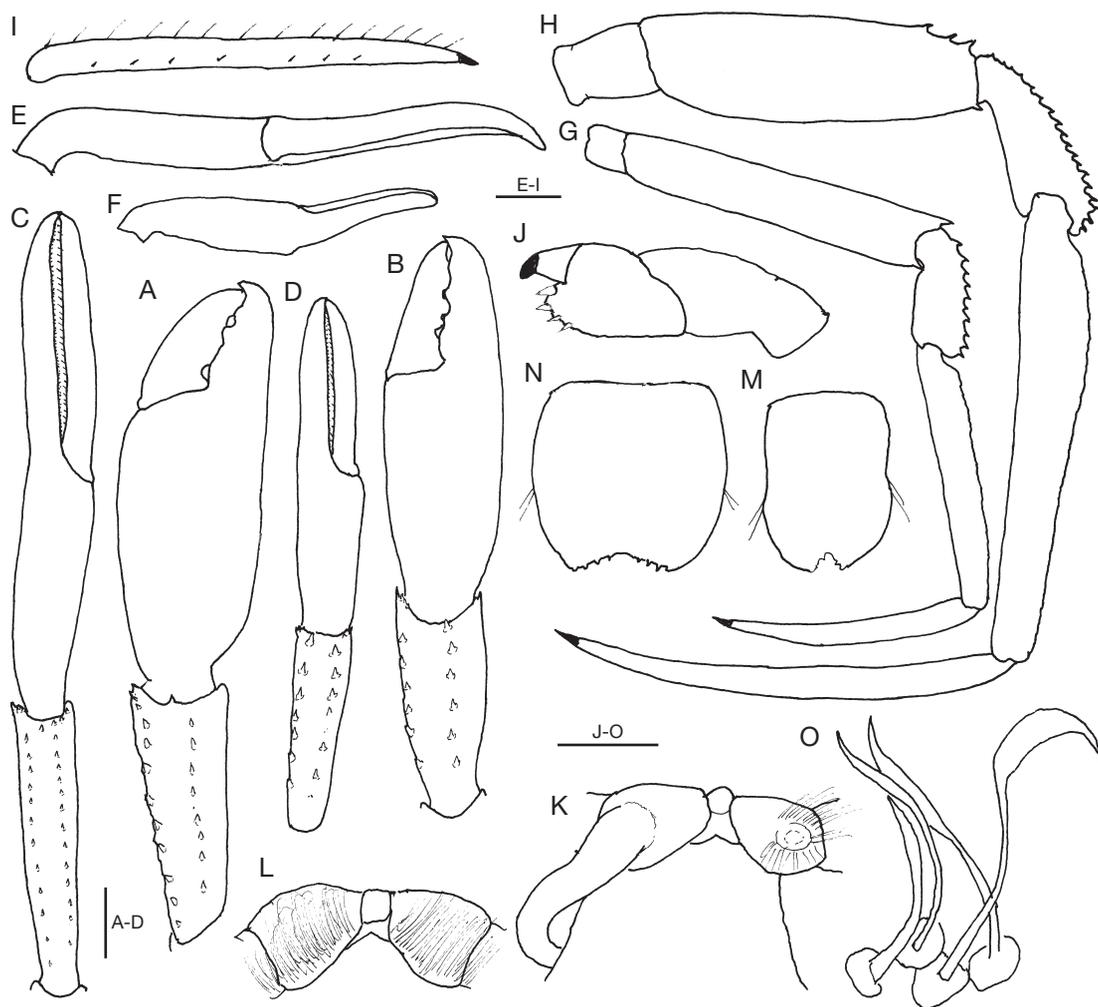


FIG. 3. — *Pteropagurus spinulocarpus* McLaughlin, 2007, EBISCO, stn DW 2492, New Caledonia (MNHN-Pg 7764): **A, B**, carpus and chela of right cheliped, dorsal view (setae omitted); **C, D**, carpus and chela of left chela, dorsal view (setae omitted); **E, F**, left chela, mesial view (setae omitted); **G**, right second pereopod, lateral view (setae omitted); **H**, right third pereopod, lateral view (setae omitted); **I**, dactyl of left third pereopod, mesial view; **J**, distal three segments of left fourth pereopod, lateral view (setae omitted); **K, L**, coxae and sternite of fifth pereopods, ventral view; **M, N**, telson, dorsal view; **O**, cluster of stalked protozoans from shell interior; **A, C, E, G-K, M**, ♂ (1.6 mm); **B, D, F, L, N**, ♀ (1.7 mm); **O**, from shell. Scale bars: 0.5 mm.

entirely fused; crista dentata (Fig. 2H) reduced to few very tiny teeth.

Right cheliped (Fig. 3A, B) slightly longer to appreciably shorter than left, but considerably stouter; dactyl and fixed finger with or without slight hiatus. Dactyl 0.6-0.7 length of palm; dorsomesial margin rounded, all surfaces unarmed, but with few scattered setae, particularly ventrally; cutting edge with 2 or

3 moderate to large calcareous teeth. Palm slightly shorter to slightly longer than carpus; dorsomesial and dorsolateral margins rounded, unarmed, convex dorsal and ventral surfaces also unarmed. Carpus slightly longer than merus; dorsomesial and dorsolateral margins each with row of 4-9 small spines, number increasing with increased animal size, other surfaces unarmed, but distomesial margin often

with 2 or 3 smaller spines. Merus glabrous or with row of widely-spaced, individual bristles on dorsal surface; other surfaces unarmed but with few scattered setae; ventromesial and ventrolateral distal angles each usually with small spine.

Left cheliped (Fig. 3C-F) long, slender, considerably longer than right with tips prominently curved in larger male specimens; dactyl and fixed finger upwardly flexed (Fig. 3F) and with slight hiatus; dactyl shorter to approximately 1.2 length of palm; surfaces all unarmed but with sparse scattering of short setae particularly ventrally. Palm long, slender, surfaces unarmed but with few scattered setae. Carpus approximately equal to length of merus; dorsomesial and dorsolateral margins each with row of small spines increasing in number with increasing body size, other surfaces unarmed but with few scattered setae.

Second (Fig. 3G) and third (Fig. 3H, I) pereopods similar in armature, but dissimilar in length and proportions, third appreciably longer and stouter. Dactyls slightly shorter to approximately equal to lengths of propodi; terminating in small corneous claws; mesial faces each with row of widely-spaced small bristles or corneous spinules adjacent to ventral margin (Fig. 3I). Propodi approximately twice length of carpi, unarmed or with very low protuberances and sparse row of setae on each dorsal surface. Carpi each with row of small spines on dorsal surface. Meri of second pereopods each usually with dorsodistal spine, occasionally unarmed; third each with 1 dorsodistal and 1-3 subdistal spinulose protuberances or small spines and 1 or 2 setae, ventrolateral distal angles each with tiny spinule or small spine. Fourth pereopods (Fig. 3J) semichelate; propodal rasp with 1 row of 3-5 spiniform corneous scales.

Sternites of second and third pereopods (Fig. 2I, J) broad; third broadly subrectangular anteriorly and drawn out posteriorly into broad, terminally rounded plate in both sexes. Sternite of fifth pereopods (Fig. 3K, L) with simple or faintly bilobed median projection in both sexes.

Male with coxae of fifth pereopods approximately equal, right with long, stout sexual tube developed as posterior coxal extension (Fig. 3K) directed posteriorly and exteriorly and curving over

anterior portion of dorsal pleon; coxa of left with gonopore and sometimes papilla. Coxae of fifth pereopods (Fig. 3L) in females each with dense setae on ventral surface.

Telson (Fig. 3M, N) with V- or U-shaped median cleft, or only slight median concavity; terminal margins oblique, each with 2-4 tiny blunt or acute spines; lateral margins each with 1 or 2 moderately long setae.

Coloration

Unknown.

Habitat

Empty shells of *Cuvierina colummella* (Rang, 1827).

Larval development

Only limited information available from prematurely hatched zoeae. Carapace with no rostral spine apparent; posterolateral angles rounded. Appendages typical of first stage zoeae, but none with setae extruded. Pleon with 5 somites and telson; posterior telsonal margin (Fig. 2K) with small U-shaped median cleft and 7+7 processes: outermost – small spine, second – anomuran hair, third through seventh – plumodenticulate setae, fourth longest.

REMARKS

The mouthparts of *P. spinulocarpus* are in general agreement with those described for *P. inermis* by McLaughlin & Rahayu (2006) as representative of the genus. However, the crista dentata of *P. spinulocarpus* consists of considerably fewer teeth than were illustrated but not specified for *P. inermis*. Although the right chelipeds of males of *P. spinulocarpus* are generally a little stouter than females, both are very similar morphologically and do not change with growth. McLaughlin's (2007) description of the left chela being ventrally curved in both sexes is misleading. In lateral or mesial view, the dactyl and fixed finger are flexed upward in relation to the ventral margin of the palm (Fig. 3F) with the ventral margins of the former slightly curved. This flexion readily distinguishes the left cheliped of *P. spinulocarpus* from the otherwise structurally similar and sexually dimorphic left

cheliped of *C. spinicarpus*. Nonetheless, the left chelipeds of *P. spinulocarpus* exhibit comparable sexual dimorphism to that seen in *C. spinicarpus*, such as an increase in length with increased animal size and the prominent ventral curvature of the distal portions of the dactyl and fixed finger, which accompanies the increase in overall length in males (Fig. 3C, E), but not in females (Fig. 3D, F). Sexual dimorphism is exhibited by females of *P. spinulocarpus* in the presence of moderately dense setation on the ventral surfaces of the coxae of the fifth pereopods (Fig. 3L).

The increases in the number of spines on the dorsal surfaces of the carpi of the chelipeds and ambulatory legs occur with increased body size in both sexes and appear to be entirely functions of growth. The variations seen in the breadth, median cleft, or armature of the telson (Fig. 3M, N) do not appear to be dimorphic or growth related.

McLaughlin & Rahayu (2006) speculated that the longer third pereopods of *Pteropagurus* species enabled the animals to elevate the shells above the substrate when walking, as none of the four shells examined in their original sample had any marks on the exterior surfaces. The numerous carciñoecia of *P. spinulocarpus* in the recent sample support their supposition. The external shell surfaces are clear and smooth, showing no signs of scuffing from being dragged across the substrate. The apertures are usually smooth and unbroken. In the preserved state, the appendages of the hermits often were at least partially extended; however, the entire animals and their appendages could be retracted completely into the carciñoecia. On the internal surfaces of several of the pteropod shells occupied by *P. spinulocarpus* were what appeared to be clusters of a stalked protozoan (Fig. 3O) probably of the phylum Ciliophora. Although Williams & McDermott (2004) indicated that protozoan attachments included shell surfaces and other symbionts as well as the exoskeletons of the crabs, Fernandez-Leborans & Tato-Porto (2000a, b) and Fernandez-Leborans (2001) reported such attachments only on the gills, integuments, and setae of several hermit crabs. Clusters similar to those on the shell walls occasionally also were observed on the bodies of *P. spinulocarpus*.

Genus *Catapagurus* A. Milne-Edwards, 1880

TYPE SPECIES. — *Catapagurus sharreri* A. Milne-Edwards, 1880 by monotypy.

Catapagurus spinicarpus

de Saint Laurent & McLaughlin, 2000
(Figs 4; 5)

Catapagurus spinicarpus de Saint Laurent & McLaughlin, 2000: 146, fig. 46. — McLaughlin 2004: 14.

HOLOTYPE. — New Zealand. Kermadec Islands BS 438, 29°14.7'S, 177°49.4'W, 165-149 m, 28.X.1975, ovig. ♀ (2.7 mm) (NMNZ Cr 9651).

NEW MATERIAL EXAMINED. — New Caledonia. EBISCO, stn 2492, 24°44.0'S, 159°41.0'E, 285 m, 6.X.2005, 30 ♂♂ (1.4-3.0 mm), 18 ♀♀ (1.5-2.8 mm), 46 ovig. ♀♀ (1.7-2.2 mm) (MNHN-Pg 7765).

DISTRIBUTION. — Kermadec Islands, New Zealand, Chesterfield Islands, New Caledonia; 149-285 m.

SUPPLEMENTAL DESCRIPTION

Shield (Fig. 4A) broader than long; surface with several tufts of setae. Rostrum broadly rounded to obtusely subtriangular, varying from not quite reaching levels of lateral projections to extending beyond. Lateral projections broadly rounded to obtusely triangular, unarmed or with marginal small spine or spinule. Ocular peduncles moderately short, broadened distally, 0.6-0.7 length of shield, dorsal surfaces each often with sparse tuft of setae at corneal indentation; corneal diameter 0.7-0.9 of peduncular length; ocular acicles narrowly triangular, slender, not quite reaching midlength of peduncles to reaching considerably beyond; terminating acutely. Antennular peduncles overreach distal margin of corneas by entire lengths of ultimate segments to 0.6 of penultimate segments. Antennal peduncles reaching distal margins of corneas to overreaching margins by 0.6 length of fifth segments. Third segment with spinule or small spine at ventrodistal angle. Second segment with dorsolateral distal angle produced, reaching proximal margin of fourth peduncular segment to nearly distal margin, terminating in acute or subacute spine; dorsomesial distal angle with spine. First segment with small to moderately

large spine on laterodistal margin, ventral margin also with prominent spine distolaterally. Antennal acicle reaching basal corneal margin to overreaching distal margin, with small terminal spinule, mesial margin with few long setae. Antennal flagella long, often overreaching outstretched chelipeds; each article usually with 2 microscopic to short setae, at least in distal half.

Mandible (Fig. 4B) with calcified cutting edge, and small corneous tooth at lower outer angle; palp 3-segmented. Maxillule (Fig. 4C) with weakly developed external endopodal lobe, internal lobe with 1 stiff bristle. Maxilla (Fig. 4D) with endopod not overreaching distal margin of scaphognathite. First maxilliped (Fig. 4E) with very slender exopod. Second maxilliped (Fig. 4F) without distinguishing characters. Third maxilliped (Fig. 4G, H) with 3 or 4 teeth on basis; crista dentata with 8-10 teeth and prominent accessory tooth; merus with dorso-distal spine.

Right cheliped (Fig. 5A-D) long, moderately slender, somewhat dorsoventrally compressed; sexually dimorphic. Dactyl 0.5-0.8 length of palm; dorsomesial margin not delimited, surfaces minutely tuberculate or spinulose and with scattered short setae, particularly ventrally; cutting edge with 2 large, widely-spaced, often denticulate, calcareous teeth interspersed with much smaller calcareous teeth, row of similar small calcareous teeth distally, terminating in tiny corneous claw and overlapped by fixed finger, at least in larger specimens of both sexes. Palm approximately equal to or slightly longer than carpus in females (Fig. 5B) and small males, considerably longer than carpus in larger males (Fig. 5A); dorsomesial margin weakly delimited at least proximally and distally, dorsolateral margin not distinctly delimited, convex surfaces all with covering of minute to tiny granules or spinules except for generally smooth dorsodistal half of fixed finger; cutting edge of fixed finger with 2 or 3 low, broad, often denticulate calcareous teeth and few smaller calcareous teeth distally, terminating in small corneous or calcareous claw; ventral surface with scattered setae. Carpus with row of slender spines on dorsomesial margin, dorsodistal margin unarmed, dorsal surface granular or minutely tuberculate, dorsolateral margin with single or double

row of slightly to considerably smaller spines; lateral and mesial faces minutely granular; ventral surface granular or tuberculate. Merus usually with small spine on dorsodistal margin, occasionally only with few stiff bristles, dorsal surface with 2 to complete row of low protuberances or very short transverse ridges, each with 1 or more short stiff bristles and occasionally small corneous spine; mesial and lateral faces microscopically granular; ventral surface tuberculate or granular; ventrolateral margin with row of tiny spinules or granules, 1 or 2 quite small spines at distal angle; rounded ventromesial margin minutely granular or spinulose, ventromesial distal angle with acute or blunt spine.

Left cheliped (Fig. 5E-H) slender, as long as right, occasionally slightly longer; somewhat dorsoventrally compressed; dactyl and fixed finger straight in females and small males (Fig. 5H), becoming ventrally arched in large males (Fig. 5G). Dactyl equaling length of palm to 1.3 longer in large specimens of both sexes; dorsomesial margin only faintly delimited and microscopically spinulose or granular, several short to moderately long setae marginally and on dorsal and ventral surfaces; cutting edge with row of tiny corneous teeth, terminating in very small corneous claw. Palm 0.6-0.8 length of carpus; rounded dorsomesial and dorsolateral margins microscopically or minutely spinulose; dorsal surface of palm and proximal 0.4-0.5 of fixed finger minutely granular; mesial and lateral faces and ventral surface microscopically granular; distal 0.5 of fixed finger with few short to moderately long setae; cutting edge with row of minute corneous teeth, terminating in tiny corneous claw. Carpus with row of slender spines on dorsomesial and dorsolateral margins; surfaces all minutely granular and with few short to moderately long setae. Merus with or without small spine at dorsodistal margin, dorsal surface with row of short transverse ridges or low protuberances, each accompanied by few stiff setae and often corneous spine, at least in large specimens; ventral surface with scattered very small tubercles, ventromesial and ventrolateral margins each weakly delimited by row of very small to tiny spinules or spinulose tubercles, ventrodistal angles each with 1 or 2 small spines. Ischium unarmed or with row of minute granules on ventromesial margin.

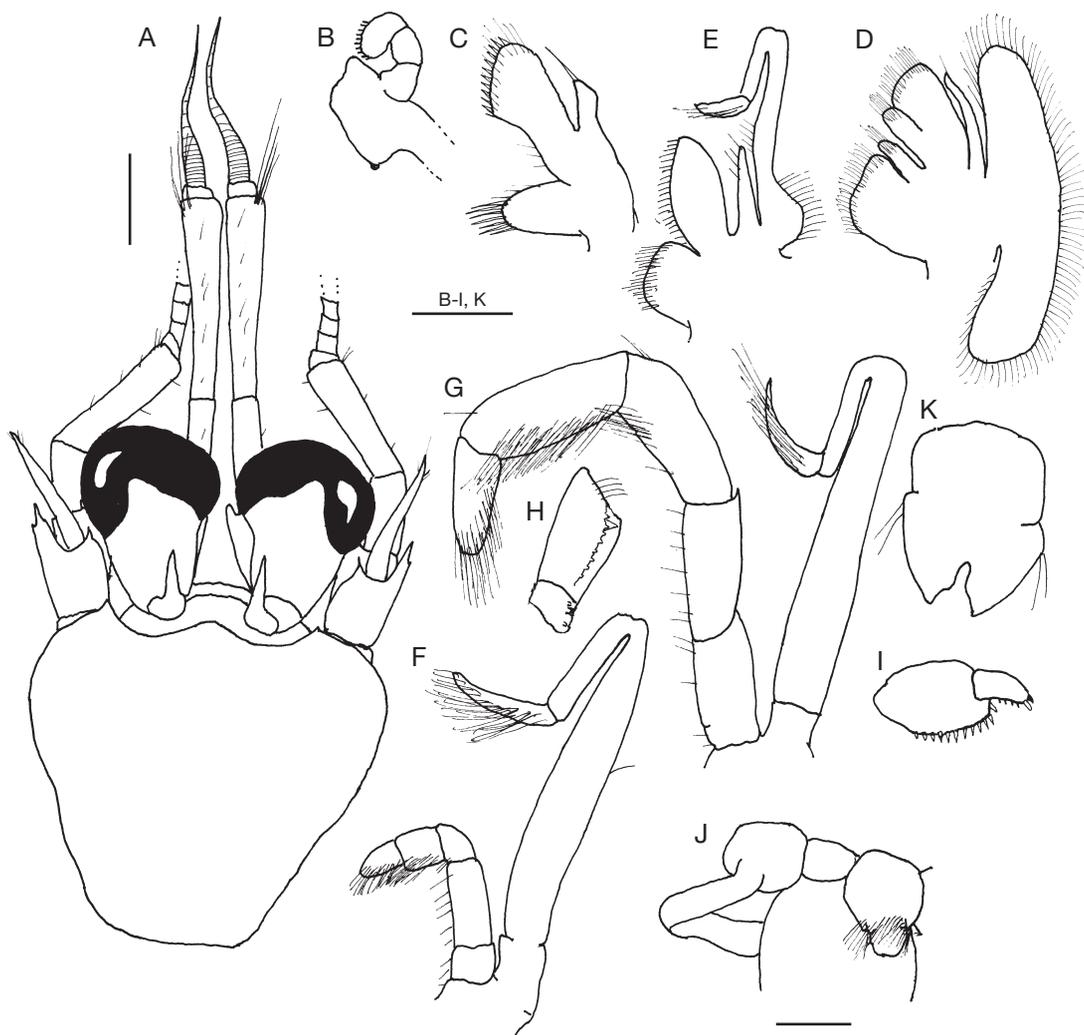


FIG. 4. — *Catapagurus spinicarpus* de Saint Laurent & McLaughlin, 2000, EBISCO, stn DW 2492, New Caledonia (MNHN-Pg 7765): **A**, shield and cephalic appendages, dorsal view (aesthetascs and most setae omitted); **B**, left mandible, outer view; **C**, left maxillule, outer view; **D**, left maxilla, outer view; **E**, left first maxilliped, outer view; **F**, left second maxilliped, outer view; **G**, left third maxilliped, outer view; **H**, ischium of left third maxilliped, inner view; **I**, propodus and dactyl of right fourth pereopod, lateral view (setae omitted); **J**, coxae and sternite of fifth pereopods, ventral view; **K**, telson, dorsal view; **A, J, K**, ♂ (3.0 mm); **B-I**, ♂ (1.8 mm). Scale bars: 0.5 mm.

Ambulatory legs (Figs 5I-K) elongate, generally similar. Dactyls not blade-shaped; in dorsal view, straight; in lateral view, curved ventrally in distal halves; 1.1 to 1.6 longer than propodi, third often longer than second but not markedly so; dorsal margins each with row of spiniform setae, longer and more bristle-like distally, but often broken off; mesial faces (Fig. 5K) each with ventral row of 14

to 25 very small corneous spinules; lateral faces with few setae; ventral margins usually glabrous, occasionally with few setae. Propodi 1.7-3.0 length of carpi; dorsal surfaces each with row of granules or tiny spinules, often accompanied by short bristle-like setae, third occasionally only with row of protuberances and short bristle-like setae; mesial and lateral faces unarmed or minutely granular;

ventromesial margins each with row of very short spiniform bristles often hardly discernable. Carpi short, 0.4-0.6 length of meri; dorsal surfaces each with sparse setae and row of small spines, lateral faces of second pereopods each occasionally with short irregular row of small spinules or tubercles; mesial and ventral surfaces usually unarmed, occasionally microscopically granular. Meri of second pereopod distinctly longer than third; each with dorsal surfaces varying from irregularly spinulose to with 1-4 short transverse ridges distally, often each with small spine or corneous spinule and/or 1-3 short bristles; ventrolateral distal angles each sometimes with very small spine or spinule, ventromesial and ventrolateral margins each with row of granules, spinules or small spines, sometimes few additional granules, tubercles or spinules on ventral surfaces. Fourth pereopods (Fig. 4I) each with very small preungual process at base of quite small claw.

Coxae of fifth pereopods in males (Fig. 4J) each with well-developed right sexual tube typical of genus; left usually with papilla or very short tube. Females with second to fourth pleopods biramous, fifth pleopods uniramous.

Uropods varying from nearly symmetrical to markedly asymmetrical; exopods much longer than endopods, each with 2 rows of scales on outer margin. Telson (Fig. 4K) with triangular posterior lobes separated by moderately deep, generally V-shaped median cleft; oblique terminal margins unarmed but often with 1-3 tiny bristles; lateral margins each sometimes with narrow chitinous marginal plate and 2 short stiff bristles near marginal indentation.

Coloration

Unknown.

Habitat

Empty pteropod shells of *Cuvierina urceolaris* (Mörch, 1850) and other snail shells primarily belonging to the family Naticidae, usually with anemones encircling shell apertures.

REMARKS

Catapagurus spinicarpus and *Pteropagurus spinulocarpus* are superficially so similar as to be easily

mistaken for one another at first glance. Both have broad shields; short, stout, distally broadened ocular peduncles with prominently dilated corneas and moderately short ocular acicles; long antennular and antennal peduncles; long slender chelipeds and ambulatory legs; and males with long right sexual tubes curved dorsally over the pleons. There are, of course, numerous generic characters that will differentiate between the two taxa. However, when both pairs of ambulatory legs are present, the marked difference in the lengths of the second and third pairs of *P. spinulocarpus* (Fig. 3G, H) will immediately distinguish this species from *C. spinicarpus* (Fig. 5I, J). Additionally, the broad and posteriorly produced sternite of the third pereopods (Fig. 2I, J) clearly identifies the former taxon. Both species exhibit sexually dimorphic growth of the left chela (Figs 3C-F; 5E-H), but only in *C. spinicarpus* is similar dimorphic growth also seen in the right chela (Fig. 5A-D).

In contrast to the clean, smooth and transparent shells of *Cuvierina columnella* occupied by *Pteropagurus spinulocarpus* and *P. spina*, the pteropod shells utilized by *Catapagurus spinicarpus* were appreciably shorter, broader, and most frequently scuffed and discolored. Such shell condition would suggest that these shells had dragged along the substrate by their occupants, not unexpected in a species incapable of complete withdrawal into its carinoecia and with ambulatory legs of approximately equal length. The shells of *P. spinulocarpus* had been identified as *Cuvierina columella*, and initially it was assumed that all occupied pteropod shells belonged to the one taxon. However, in her monographic review of the pteropod family Cavaliniidae Fischer, 1883, Rampal (2002) distinguished between *Cuvierina columnella* and *C. urceolaris* by shell length and breadth in addition to morphological attributes of the animals. She noted that although they were found sympatrically there was no indication of hybridization. The shells occupied by *Catapagurus spinicarpus* agree well with the measurements, description and figures of *Cuvierina urceolaris* provided by Rampal (2002: 210, fig. 1A), whereas the shells utilized by the *Pteropagurus* species agree with her (p. 211, fig. 1B) description and illustrations of *Cuvierinia columella*. With only the empty shells

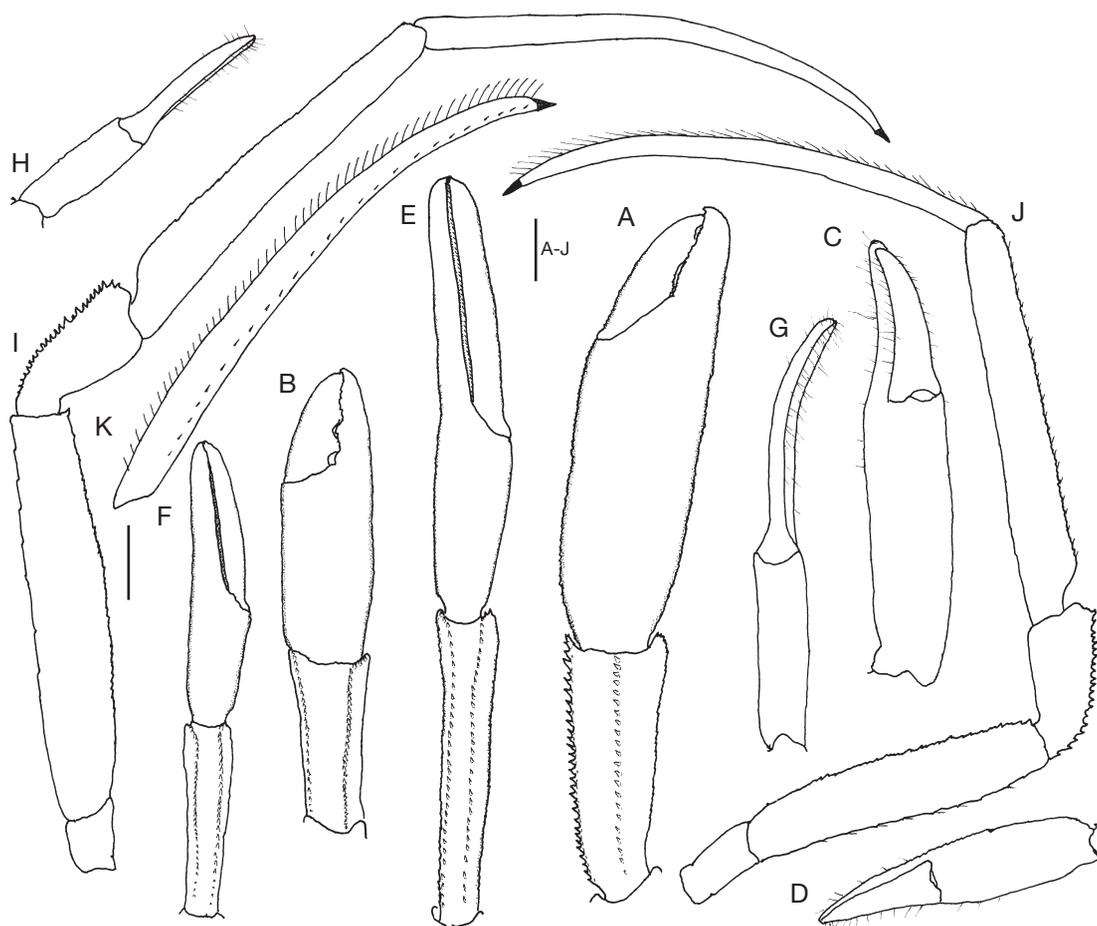


FIG. 5. — *Catapagurus spincarpus* de Saint Laurent & McLaughlin, 2000, EBISCO, stn DW 2492, New Caledonia (MNHN-Pg 7765): **A, C**, carpus and chela of right cheliped, dorsal view (setae omitted); **B, D**, chela of right cheliped, mesial view; **E, G**, carpus and chela of left cheliped, dorsal view (setae omitted); **F, H**, chela of left cheliped, mesial view; **I**, right second pereopod, lateral view (setae omitted); **J**, left third pereopod, lateral view; **K**, dactyl of left third pereopod, mesial view; **A, C, E, G, I-K**, ♂ (3.0 mm); **B, D, F, H**, ♀ (2.5 mm). Scale bars: 1 mm.

available, the specific identities of the pteropods can only be considered tentative; however, one of the areas of sympatry of the two pteropods is New Caledonia.

The majority of specimens of *Catapagurus spincarpus* still retaining the carcinocelia during preliminary examination were ovigerous females, with only their pleons inserted into the shells. Nevertheless, despite the only weakly swollen lumens of the shells, the hermits were not easily removed. Their eggs, although attached in a typical manner to the left second

through fourth pleopods, were carried ventrally and sometimes dorsally as well as on the left side of the pleon, thus completely filling the interiors of the shells. Additionally, and as has been observed in the *Pteropagurus* species, *C. spincarpus* pteropod shell inhabitants carried the uropods and telson tucked under the posterior portion of the pleon. The apertures of these shells almost always had remnants of previously attached anemones, but occasionally after the shell had been dislodged, the anemone remained encircling the pleon of the crab.

DISCUSSION

In their review of information gathering by hermit crabs, Elwood & Neil (1992) briefly summarized hermit crab behavior by saying that [snail] shells are an extremely important resource; that having of the correct species and size of shell can increase survivorship and reproduction; and that competition over shells is often intense. Numerous studies have been conducted to examine the influence of shell size and shape on growth and reproduction in shallow-water hermit crab species (e.g., Fotheringham 1976b, 1980; Scully 1979; Bertness 1981a; McClintock 1985; Blackstone 1986; Gherardi 1991; Angel 2000; Benvenuto & Gherardi 2001), and all concur that ill-fitting shells affect crab vigor. Because shell resource limitations reportedly occur among numerous intertidal hermit crab species (e.g., Vance 1972; Fotheringham 1976a; Abrams 1980, 1981; Bertness 1981b; Blackstone 1985; Gerardi 1990; Busato *et al.* 1998), it would be reasonable to suspect that despite depth differences, the use of empty pteropod shells by *Catapagurus spinicarpus* was a response to snail shell resource limitations. In the absence of appropriate snail shells, hermit crabs, particularly juveniles, have been reported to resort to variety of unusual shelters from hollow fragments of brown algal rhizoids to brachyuran eye exuvia (Đuriš 1992). Regrettably, data not available regarding snail shell abundance at the EBISCO station preclude a definitive answer regarding *C. spinicarpus*' occupancy. However, Benvenuto & Gherardi (2001) concluded that the hermit crab populations in their study were able to choose shells of a given morphology, size and status, with females preferring lighter shells.

Although *Pteropagurus spinulocarpus* appeared to be restricted to the use of shells of the pteropod *Cuvierina columella*, *Catapagurus spinicarpus* was not similarly limited. In the same sample, the *Catapagurus* species also was found occupying shells of snails of the family Naticidae and juvenile shells not readily identifiable as well, but in far fewer numbers. Nonetheless, most of the *C. spinicarpus* occupants of the pteropod shells were ovigerous females. However, as previously indicated, whether the carcinoecium was a pteropod or snail shell,

C. spinicarpus most frequently was associated with an anemone of undetermined identity. A similar hermit-anemone relationship was not observed in either *Pteropagurus* species. It might be speculated that the protection provided by the anemone (cf. Williams & McDermott 2004) to the less well-adapted *C. spinicarpus* was not needed by the species of *Pteropagurus*, which were able to retract completely into their carcinoecia.

Catapagurus species routinely occupy shells with very short spires (McLaughlin personal observation), and consequently do not exhibit the markedly dextrally twisted pleons common to many pagurids. Imafuku & Ando (1999) reported that the pleon of *Pagurus imafukui* McLaughlin & Konishi, 1994, a pagurid that routinely used a straight tusk shell rather than a dextrally coiled shell, nonetheless exhibited some amount of dextral pleonal twist when the crab was without its shell. Is it possible that a shortage of empty snail shells and an excess of empty pteropod shells led "desperate" specimens of *C. spinicarpus* to adopt this alternative habitat? Perhaps; however, in addition to the morphological changes observed in some, but not all of the specimens of *C. spinicarpus*, the apparently exclusive selection shells of *Cuvierina urceolaris* over *C. columella* suggests that occupancy may have been one of choice and not short term "homelessness". For example, the four ovigerous females still remaining in their pteropod carcinoecia at the time of detailed examination were found to have straight, stout, shortened pleons and nearly symmetrical uropods. Unfortunately, the majority of specimens were shell-less at the time of that examination. Nevertheless, among those were individuals with straight, stout short pleons and nearly symmetrical pleopods and individuals with weakly twisted, moderately slender, elongate pleons and markedly asymmetrical pleopods. There were also specimens with straight, stout, short pleons and asymmetrical uropods. As Harvey (1998) demonstrated, the transition from pleon asymmetry to symmetry takes place gradually through several molts, and as was shown by Rodrigues *et al.* (2002), habitat has a direct influence on uropod symmetry. The presence of anemones was restricted to the shells of *Cuvierina urceolaris*, indicating that these had been occupied by

Catapagurus spinicarpus rather than *Pteropagurus spinulocarpus*. The straightening and shortening of the pleon together with the pleonal transition from asymmetry to near symmetry does not unequivocally support the hypothesis that *C. spinicarpus* selected pteropod shells in preference to snail shells, but it does demonstrate the morphological plasticity of this species. The large number of ovigerous females of both *P. spinulocarpus* and *C. spinicarpus* would suggest that fitness and fecundity were not adversely affected by the observed sympatry between *Pteropagurus* and *Catapagurus* and would support the proposition of mutual sharing of an unusual resource rather than competition.

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