Article

ZOOTAXA

A remarkable new crab-like hermit crab (Decapoda: Paguridae) from French Polynesia, with comments on carcinization in the Anomura

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Abstract

Patagurus rex **gen. et sp. nov.**, a deep-water pagurid hermit crab, is described and illustrated based on a single specimen dredged from 400 m off Moorea, Society Islands, French Polynesia. *Patagurus* is characterized by a subtriangular, vaulted, calcified carapace, with large, wing-like lateral processes, and is closely related to two other atypical pagurid genera, *Porcellanopagurus* Filhol, 1885 and *Solitariopagurus* Türkay, 1986. The broad, fully calcified carapace, calcified branchiostegites, as well as broad and rigidly articulated thoracic sternites make this remarkable animal one of the most crab-like hermit crabs. *Patagurus rex* carries small bivalve shells to protect its greatly reduced pleon. Carcinization pathways among asymmetrical hermit crabs and other anomurans are briefly reviewed and discussed.

Key words: Decapoda, Paguridae, hermit crab, deep-water, carcinization, *Porcellanopagurus*, *Solitariopagurus,* Indo-West Pacific

Introduction

Carcinization, or development of a crab-like body plan, is a term describing an important evolutionary tendency within the large crustacean order Decapoda. The term "carcinization" was coined by Borradaile (1916) with reference to crab-like modifications in the hermit crab genus *Porcellanopagurus* Filhol, 1885 (Paguridae). However, the concept of carcinization originates with Boas' hypothesis (Boas 1880a, 1880b) that king crabs (Lithodidae[1]) represent highly derived, heavily calcified, shell-less hermit crabs. Several morphological transformations are involved in carcinization, the most conspicuous and important being the flattening, broadening, and sclerotization of the cephalothorax, and reduction and underfolding of the pleon (McLaughlin & Lemaitre 1997). Among Recent decapods, carcinization exists in various degrees only in Anomura (squat lobsters, hermit crabs, king crabs, porcelain crabs, mole crabs etc.) and Brachyura (true crabs).

The large family Paguridae includes mostly non-carcinized hermit crabs. Typical pagurids have a weakly to moderately sclerotized carapace and a soft abdomen protected by a domicile, such as a gastropod shell, scaphopod shell, or hard polychaete tube (McLaughlin & Lemaitre 1993; McLaughlin & Konishi 1994). Partly carcinized forms are known only in a few pagurid genera, most notably *Porcellanopagurus, Solitariopagurus* Türkay, 1986, and *Ostraconotus* A. Milne Edwards, 1880 (Borradaile 1916; Türkay 1986; McLaughlin 2000). These genera are characterized by a squarish, well-sclerotized carapace, a more or less reduced abdomen, and (when known) a domicile consisting of a bivalve or a limpet shell (Poupin & McLaughlin 1996; McLaughlin 2000; Martin *et al.* 2009).

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1. Throughout this paper we use king crabs and Lithodidae interchangeably to refer to the clade of decapods referred to in recent publications as the Lithodoidea. Kieler et al (2013) noted that "the term Lithodoidea … to describe a superfamily comprising Lithodidae and Hapalogastridae, however, is problematic ... both linguistically and taxonomically due to the king crabs' phylogenetically supported position within the (superfamily) Paguroidea." Therefore, we here follow the traditional concept of Lithodidae (with Lithodinae and Hapalogastrinae as subfamilies) until the classification of the Paguroidea is appropriately addressed.

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In 2009, a remarkable, fully carcinized hermit crab was collected by a Warén dredge at a depth of 400 m off Moorea Island, Society Islands, French Polynesia. This specimen superficially resembled species of *Porcellanopagurus* and *Solitariopagurus*, especially in the sclerotization of the carapace. The most unusual features of this specimen were the almost completely sclerotized carapace, with an abundance of tubercles on dorsal surface and strongly expanded lateral lobes, and a greatly reduced pleon concealed by a small bivalve shell. The unique combination of these and other features suggests that this hermit crab represents a distinct lineage in the phylogenetic proximity of *Porcellanopagurus* and *Solitaripagurus*. Therefore, a new pagurid genus is established below to accommodate this species, one of the most striking and distinctive hermit crabs discovered in the last decades.

The holotype is deposited in the Invertebrate Zoology collections of the Florida Museum of Natural History, University of Florida, Gainesville, FL, USA (UF). The terminology used in the generic and specific descriptions generally follows McLaughlin (2000). Shield (rather than carapace) length (sl), measured in mm from the tip of the rostrum to the midpoint of the cervical groove, is given as an indication of body size to be comparable to measurements provided for other pagurids.

Taxonomy

Family Paguridae Latreille, 1802

Patagurus gen. nov.

Diagnosis. Anterior carapace vaulted, well calcified, gastric region slightly elevated; rostrum subtriangular; lateral margins each developed into two relatively small, subacute lobes; cervical groove clearly delineated; posterior carapace lobes very prominent, laterally projecting; posterior carapace calcified except for a narrow, posterior, membranous band tucked under calcified portion; branchiostegite with two large and two small calcified plates. Ocular acicles vestigial. Third maxillipeds with well-developed crista dentata and one accessory tooth. Ambulatory (second and third) pereopods similar, slender, with elongate dactyli. Fourth pereopod with rasp comprised of a single row of long, slender spines. Fifth pereopod non-chelate, with no discernible rasp and very small dactylus. Thoracic sternites rigidly articulated through sternite VII. Males with elongate right sexual tube directed mesially, left sexual tube shorter and stouter than right tube, both calcified and with long tuft of setae distally. Pleon narrow, elongate, segmentation of anterior pleomeres not discernable (tergal plates not delineated), segmentation of fifth pleomere faintly discernible, sixth tergite clearly defined, but feebly calcified; male pleopods 2–5 absent. Uropods well developed, symmetrical. Telson subquadrate, entire, folded firmly against ventral surface of sixth pleomere; position of anus not determined. Female characters presently unknown.

Type species. *Patagurus rex* **sp. nov.**, by present designation.

Etymology. The new genus is named after one of the world's most eminent carcinologists, the late Dr. Patsy (Pat) A. McLaughlin (1932–2011). The generic name is a combination of McLaughlin's preferred first name and the Greek word *pagourus* (a kind of crab), which was the origin for the nominal pagurid genus, *Pagurus* Fabricius, 1775.

Remarks. The number of gills, one of the differentiating characters between *Porcellanopagurus* (11 pairs) and *Solitariopagurus* (10 pairs), could not be determined in *Patapagurus*, because penetration of the calcified branchiostegites would have resulted in serious damage to the branchial region of the single holotype specimen. The dorsal surface of the carapace of *Patagurus* (Fig. 1C) is most similar to those of species of *Porcellanopagurus* (Fig. 1A): they both generally have a pair of small lateral projections, two pairs of relatively small anterior carapace lobes, and a pair of more prominent posterior carapace lobes, which are posterior to, and clearly separated by, the cervical groove. However, the sclerotization of the posterior carapace is much more extensive in *Patagurus*, leaving only a narrow, posterior, membranous band. In contrast, *Solitariopagurus* (Fig. 1B) has a pair of strong lateral projections, three pairs of anterior carapace lobes, and a pair of small posterior carapace lobes. The dorsal surface of the shield is unarmed in all species of *Porcellanopagurus* (e.g., Borradaile 1916; Martin *et al.* 2009; McLaughlin 2000), as well as in the type species of *Solitariopagurus*, *S. profundus* Türkay, 1986. In the remaining three species of *Solitariopagurus*, the shield is armed with a row of large tubercles behind the anterior margin and

occasionally also by a few smaller tubercles elsewhere (Poupin & McLaughlin 1996; McLaughlin 1997; McLaughlin 2000; Martin *et al.* 2009). *Patagurus* (Fig. 1C) not only has the surface of the shield, but also the surfaces of the well-developed posterior carapace lobes covered with an abundance of tubercles of various sizes. Although the posterior carapace is well developed in all species of *Porcellanopagurus*, it is reduced in members of *Solitariopagurus* and presumably partly reduced and partly fused to the posterior lobes in the type species of *Patagurus*.
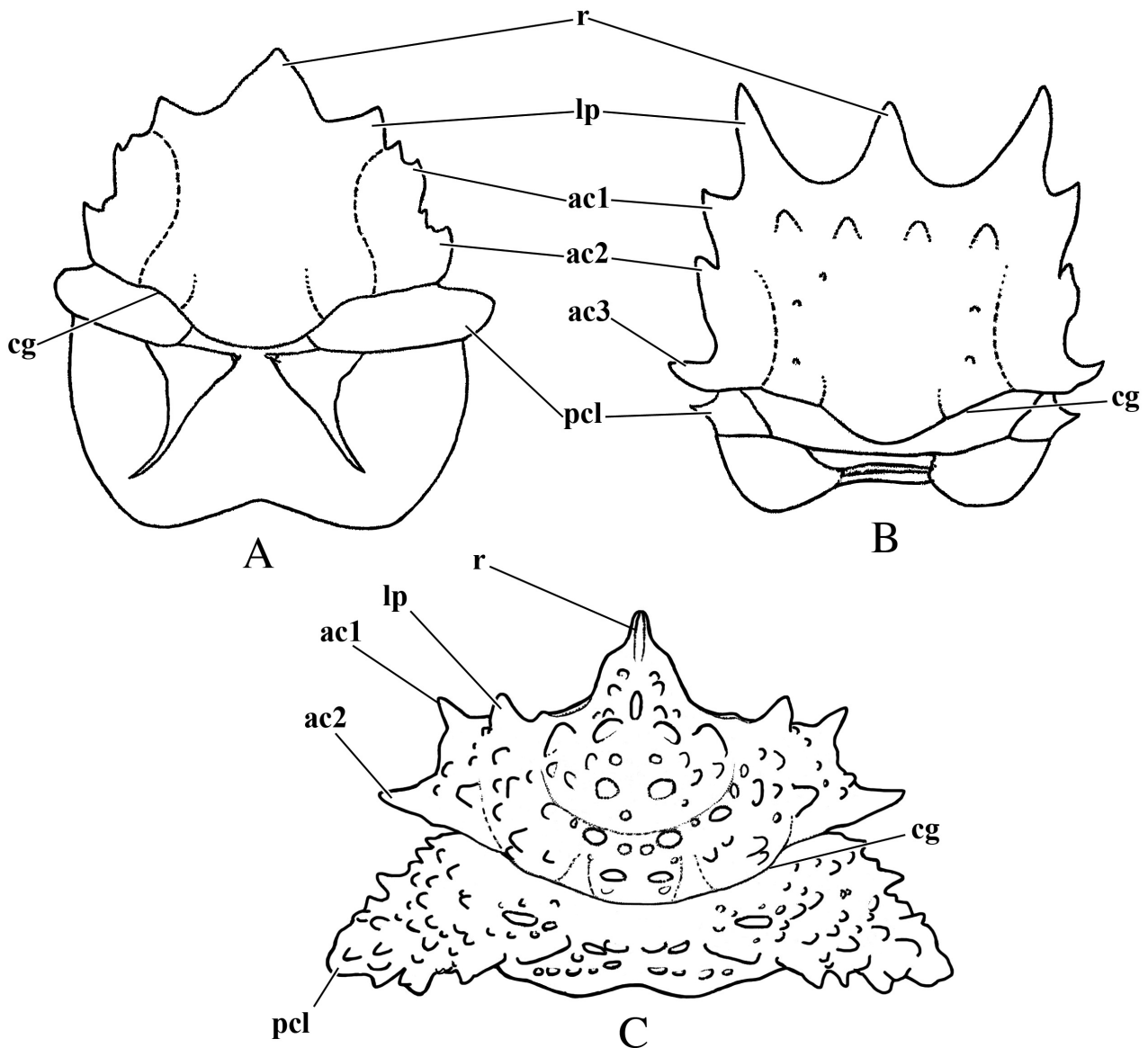

FIGURE 1. Diagrammatic dorsal view of cephalothorax in three similarly carcinized pagurid genera: A, *Porcellanopagurus*; B, *Solitariopagurus*; C, *Patagurus* **gen. nov.** Figures not to scale. Abbreviations: ac1, ac2, ac3, first, second and third anterior carapace lobes; cg, cervical groove; lp, lateral projection; pcl, posterior carapace lobe; r, rostrum.

The thoracic sternites of *Patagurus* are quite similar to those of *Solitariopagurus* and both differ considerably from the sternites of *Porcellanopagurus*. In *Patagurus* and *Solitariopagurus*, sternites III through VII are broad and rigidly articulated, with sternite VII flexed dorsally at a right angle relative to sternite VI. Similarly, asymmetrically paired male sexual tubes are seen in *Patagurus* and in all four species of *Solitariopagurus*, but are lacking in all species of *Porcellanopagurus*. Although nothing is known about the female secondary sexual characters of *Patagurus*, females of *Porcellanopagurus* all have paired gonopores, whilst females of *Solitariopagurus* have only a single left gonopore. Propodal rasps are present on the fifth pereopod in *Solitariopagurus*, but are lost in

Patagurus. Rasps on the fourth pereopod are modified to a single row of sharp, corneous spines in both genera, rather than well-developed as in most pagurids.

In species of *Porcellanopagurus* and *Solitariopagurus*, even in the largest specimens examined (McLaughlin 2000; de Saint Laurent & McLaughlin 2000), the right cheliped was not shorter than the left, as is the case in the male of the type species of *Patagurus*.

The number and type of gills and several important female characters remain unknown for *Patagurus*. Therefore, and in the absence of a more complete phylogenetic data for the family Paguridae, speculations of the phylogenetic relationship of *Patagurus* with *Porcellanopagurus* and *Solitariopagurus* would be premature. *Porcellanopagurus*, *Solitariopagurus* and *Patagurus* share numerous synapomorphies and appear to form a morphologically distinctive clade. However, the phylogenetic position of this clade within the large and heterogeneous family Paguridae remains poorly understood. There is at least an indication of some affinity of *Porcellanopagurus* and *Solitariopagurus* to several other pagurid genera characterized by a more or less calcified posterior carapace, reduced abdomen and absence of pleopods in males, especially *Ostraconotus* (McLaughlin & Lemaitre 1997) (see Discussion). *Porcellanopagurus* was included in recent phylogenetic analysis of anomurans (Schnabel *et al.* 2011, Bracken-Grissom *et al.* 2013) and recovered well within the Paguridae, sister to a clade comprised of several northern temperate Paguridae and representative king crabs.

Patagurus rex sp. nov.
(Figs. 1C, 2–6)

Type material. Holotype male (sl 5.1 mm), UF 23548, French Polynesia, Society Islands, Moorea, R/V *Alis* sta. DW 3471, 149.9167°W, 17.4833°S, Warén dredge, depth 400 m, mud and rocks, some shells, leg. G. Paulay *et al.*, 21 October 2009.

Description. Shield (Figs. 1C, 2A) considerably wider than long; anterior margins between rostrum and lateral projections broad, each with slight median protrusion; lateral projections (Fig. 2B) widely separated, moderately developed, subacute. Rostrum subtriangular, prominently drawn out into appreciably narrower tip with a mid-dorsal ridge. Anterolateral margins of shield developed as subrectangular protrusions with relatively small first and second anterior carapace lobes (Fig. 2A). Posterior carapace lobes extremely developed, sclerotized, subtriangular, each with dentate anterior margin; a narrow membranous portion, completely concealed in dorsal view, remaining near posterior margin of carapace. Dorsal surface of carapace with abundant tubercles and ridges of various sizes and shapes as illustrated (Figs. 2A, B, 4A). Branchiostegite with two large and two small calcified plates (Fig. 4E). Ocular peduncles about 0.2 shield length, each distinctly swollen in proximal half; corneas approximately half peduncular length. Ocular acicles very small, hidden in dorsal view by proximally broadened margins of rostrum.

Antennular peduncle (Figs. 2B, C) considerably longer than antennal peduncle, overreaching distal corneal margin by more than full length of ultimate segment, unarmed, but with several long setae on distodorsal margin of ultimate segment (omitted from Fig. 2C). Antennal peduncle (Figs. 2B, D) overreaching distal corneal margin by at least full length of ultimate segment, but considerably shorter than antennular peduncle; epistomial plate and first peduncular segment unarmed and lacking setae; second segment with dorsolateral distal angle produced, unarmed and terminally subacute; third through fifth segments each with few short setae; antennal acicle reaching to distal margin of fourth peduncular segment, unarmed, terminally blunt.

Mouthparts not removed. Third maxilliped with basis armed with subdistal tooth on mesial surface; ischium with well-developed crista dentata and one accessory tooth (Fig. 2E); merus, carpus, propodus and dactylus unarmed.

Thoracic sternite III prominently produced anteriorly into two triangular, subacute lobes, each with distinctly elevated, oblique ridge (Fig. 4C, D). Sternite IV roundly subrectangular, unequally divided into anterior and posterior portions by broad suture; posterior portion rigidly articulated with sternite V (Fig. 4D). Sternite VI narrow, rigidly articulated with sternite VII at ~90° angle, latter extending dorsad. Sternite VIII narrow, anterodorsal to sternite VII, separated from latter by membranous area.

Right cheliped much larger and more robust than left cheliped, but slightly shorter in overall length; propodo-carpal articulation perpendicular to main axis of cheliped, without pronounced rotation (Fig. 4B, 5B). Chela (Fig. 3C, 4B) approximately as long as carpus; dorsal surface convex, smooth, drawn out mesially and laterally into thin margins; ventral surface of palm and dactylus with scattered fine setae; dactylus approximately 0.6 length of palm,
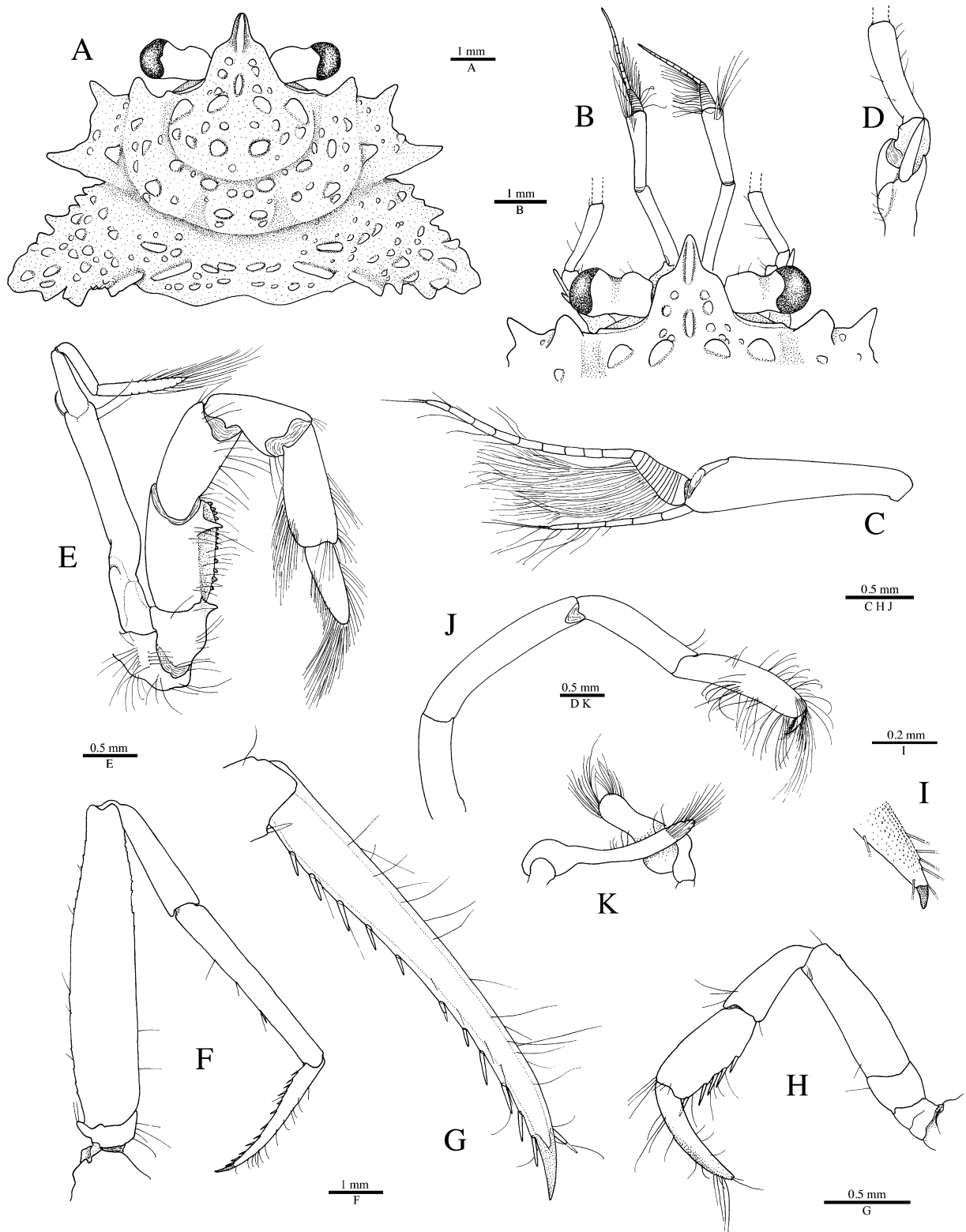
FIGURE 2. *Patagurus rex* **gen. & sp. nov.**, holotype male (UF 23548): A, cephalothorax and eyestalks (dorsal view); B, anterior portion of carapace and cephalic appendages (dorsal view); C, ultimate segment and flagellum of left antennular peduncle (lateral view, dorsolateral distal tuft of setae on ultimate segment omitted); D, left antennal peduncle (lateral view); E, right third maxilliped (ventrolateral view); F, right first ambulatory leg (lateral view); G, same, dactylus; H, left fourth pereopod (lateral view); I, same, tip of dactylus (mesial view); J, right fifth pereopod (lateral view); K, sexual tubes (posterior view).
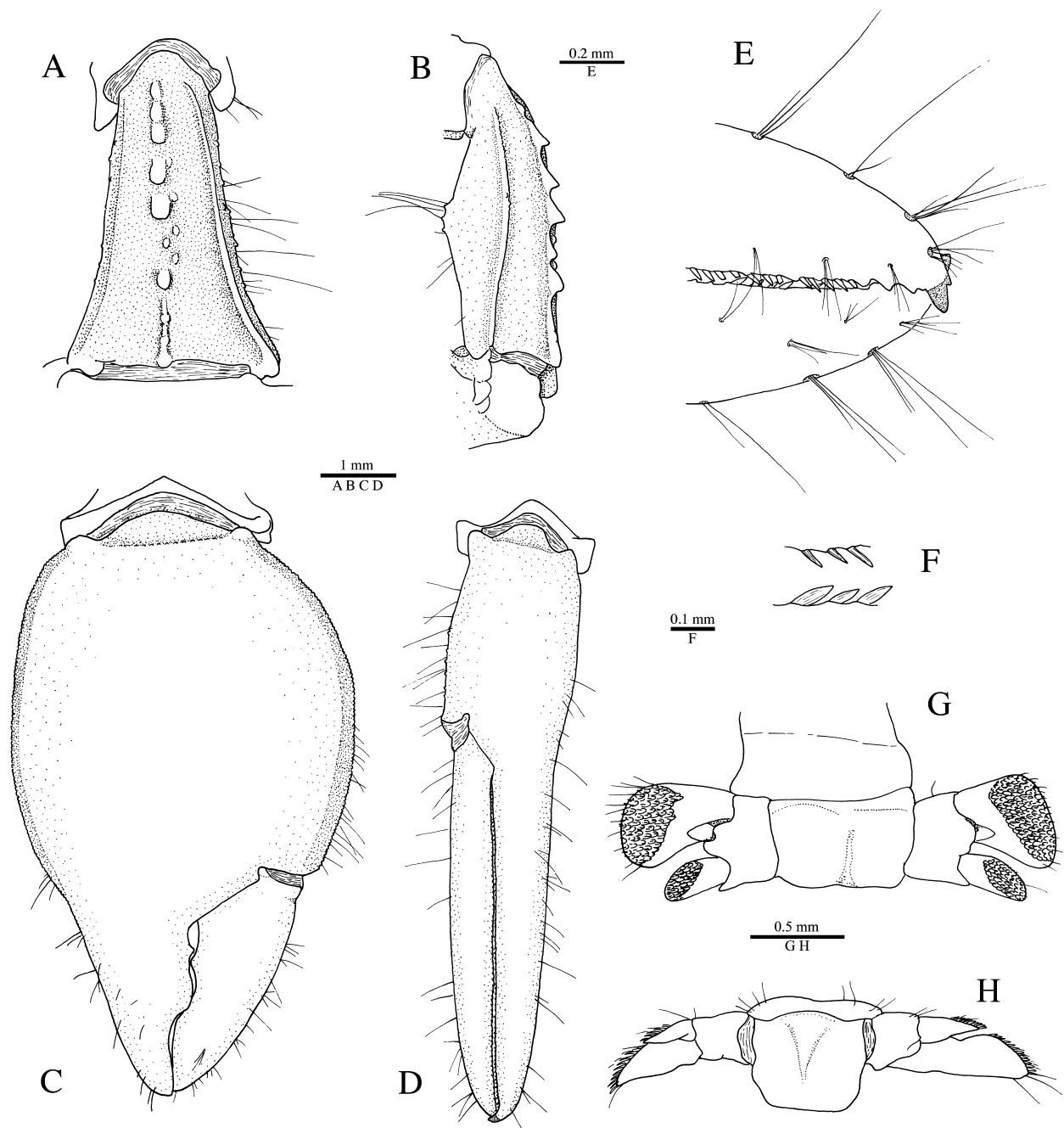
FIGURE 3. *Patagurus rex* **gen. & sp. nov.**, holotype male (UF 23548): A, carpus of right cheliped (dorsal view); B, same (lateral view); C, chela of right cheliped (dorsal view); D, chela of left cheliped (dorsal view); E, same, distal portion of fingers (ventral view); F, same, detail of dentition of cutting edges (ventral view); G, distal portion of pleon with sixth somite and uropods (dorsal view, telson not visible); H, telson and uropods (dorsal view).

unarmed, with rounded margins, some scattered setae present; cutting edges of dactylus and fixed finger calcareous, each with two low teeth, proximal larger than distal; fingers proximally gaping when closed; fingertips with small corneous point. Carpus (Fig. 3A, B) approximately as long as merus, trapezoidal, with dorsomesial and dorsolateral margins each elevated into low, unarmed crest, dorsal surface elevated in midline and with median row of tubercles, forming a distinctly rounded ridge distally; ventral surface with scattered, moderately long setae. Merus roundly triangular; lateral surface minutely granular; ventromesial and ventrolateral margins each with row of spinulose tubercles, ventral surface with some larger tubercles, smaller granules and fine setae. Ischium with faint rugosities or granules mesially, remaining surface unarmed.
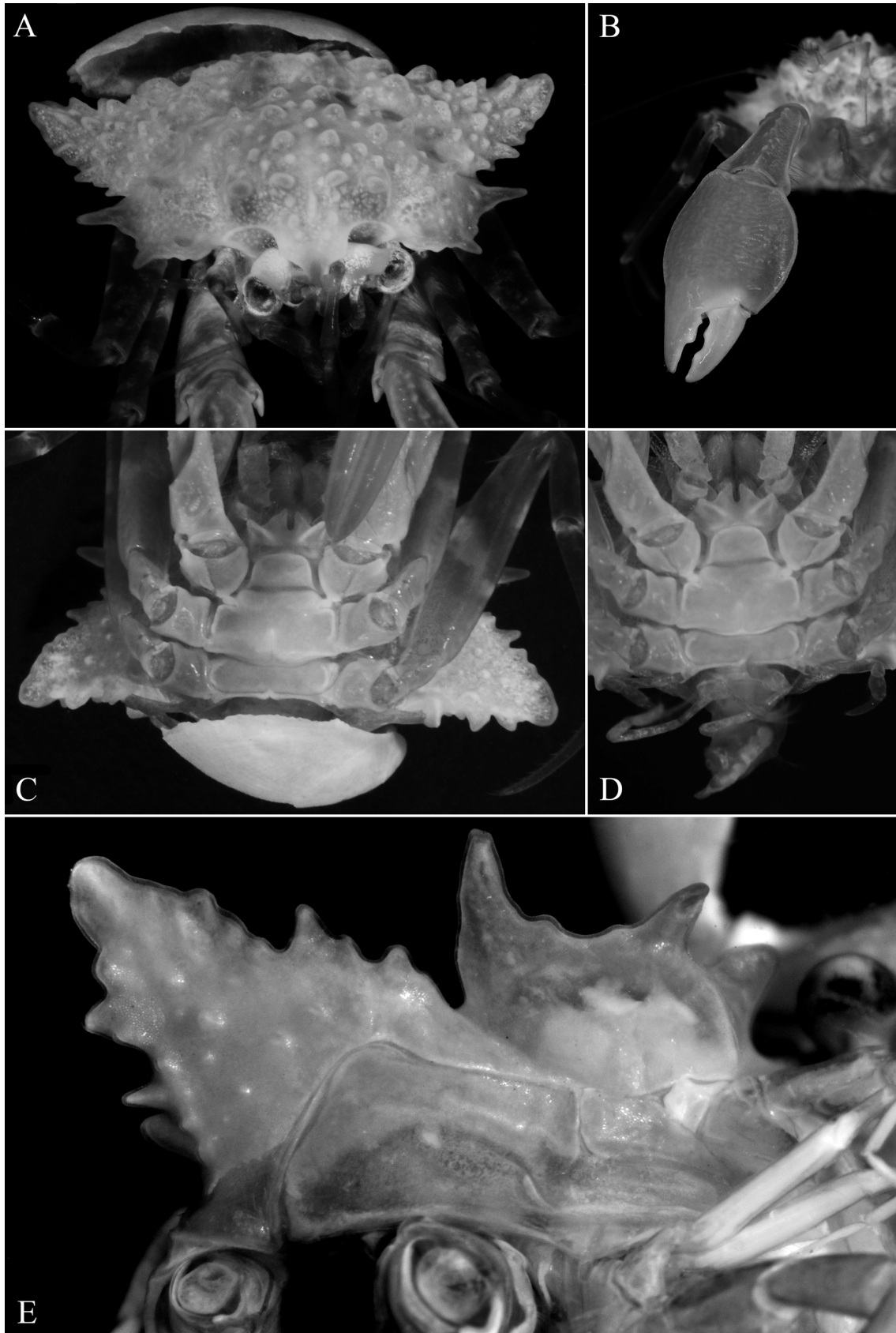
FIGURE 4. *Patagurus rex* **gen. & sp. nov.**, holotype male (UF 23548): A, anterodorsal view of cephalothorax with eyes, cephalic appendages, and part of chelipeds; B, right cheliped *in situ* (dorsal view); C, ventral view of cephalothorax and pleon, latter concealed by bivalve shell *Gregariella* sp.; D, sternum and pleon without bivalve shell (ventral view); E, branchiostegial area of cephalothorax, lateral view.

FIGURE 5. *Patagurus rex* **gen. & sp. nov.**, holotype male (UF 23548), habitus and coloration in dorsal view (shell detached). Photograph: Arthur Anker.

Left cheliped elongate, slender; dactylus and fixed finger distinctly arched ventrally. Chela shorter than carpus; dorsal surface unarmed, slightly convex, with rounded margins; ventral surface with numerous tufts of moderately long setae on palm and especially on fixed finger; cutting edge of fixed finger with row of small corneous teeth; dactylus more than twice length of palm, unarmed, with tufts of moderately long setae; margins rounded; cutting edge with row of minute corneous teeth (Fig. 3D–F). Carpus approximately equal to merus length; dorsomesial and dorsolateral margins each elevated into unarmed crest; dorsal surface elevated in midline and armed with row of subacute spiniform tubercles; lateral face minutely granular; ventral surface with scattered small tubercles and moderately long setae. Merus roundly triangular; lateral surface minutely granular; ventral surface with irregular row of spinulose tubercles adjacent to lateral margin, some tubercles and fine setae present on ventral surface and mesially. Ischium unarmed.

Ambulatory legs (second and third pereopods) similar in shape and length (Figs. 2F, 5). Dactyli slightly shorter than propodi, each with sparse, moderately long setae dorsally and one corneous spinule adjacent to terminal corneous unguis; mesial and lateral faces with few shorter, scattered setae; ventral margins each with row of 11 or 12 corneous spines (Fig. 2G). Propodi approximately 1.5 length of carpi, unarmed, with scattered setae. Carpi short, slightly less than 0.5 lengths of meri; unarmed, with few scattered setae. Meri unarmed except for minute protuberances on ventral margin. Ischia unarmed; lengths of ischium of second and third pereopods similar.

Fourth pereopod (Fig. 2H) with dactylus and propodus bearing scattered setae; dactylus somewhat sickle-shaped, about as long as propodus, covered with minute tubercles (Fig. 2I); propodal rasp consisting of single row of five, long corneous spines; carpus and merus unarmed, each with few setae. Fifth pereopod (Fig. 2J) with very small dactylus obscured by terminal tufts of long setae originating from propodus, without rasp. Coxae of male fifth pereopods each with well-developed sexual tube, right longer and more slender, both densely setose distally (Fig. 2K).

Male pleon markedly reduced (Figs. 4D, 5C, E), lacking pleopods 2–5. Uropods symmetrical; endopod and exopod each with ovate rasp of corneous scales, exopodal rasps larger than endopodal rasps (Fig. 3G). Telson

subquadrate, with trace of lateral indentation; dorsal surface proximally with median depression; posterior margin entire, unarmed (Fig. 3H).

Female unknown.

Color in life. Calcified portions of carapace hyaline-whitish with scattered tints of orange and pink; tip of rostrum and first and second anterior carapace lobes darker orange; ocular peduncles white; antennular and antennal peduncles and flagella orange; ventral cephalothorax pale orangish-white; chelipeds bright orange dorsally, lighter orange ventrally; ambulatory legs with orange dactyli, propodi and carpi each reddish-orange with white band at distal margin, meri reddish-orange, each with irregular splotches of white (Figs. 5, 6).

Etymology. Referring to the extraordinary albeit superficial resemblance of this new species to some king crabs (*rex* = king in Latin).

Distribution. Presently known only from the type locality off Moorea, Society Islands, French Polynesia.

Habitat. Mud and rocks bottom at a depth of 400 m.

Biological notes. The hermit crab was covering its miniature abdomen with a valve of the mytilid bivalve, *Gregariella* sp. (Figs. 4C, 6A, B).
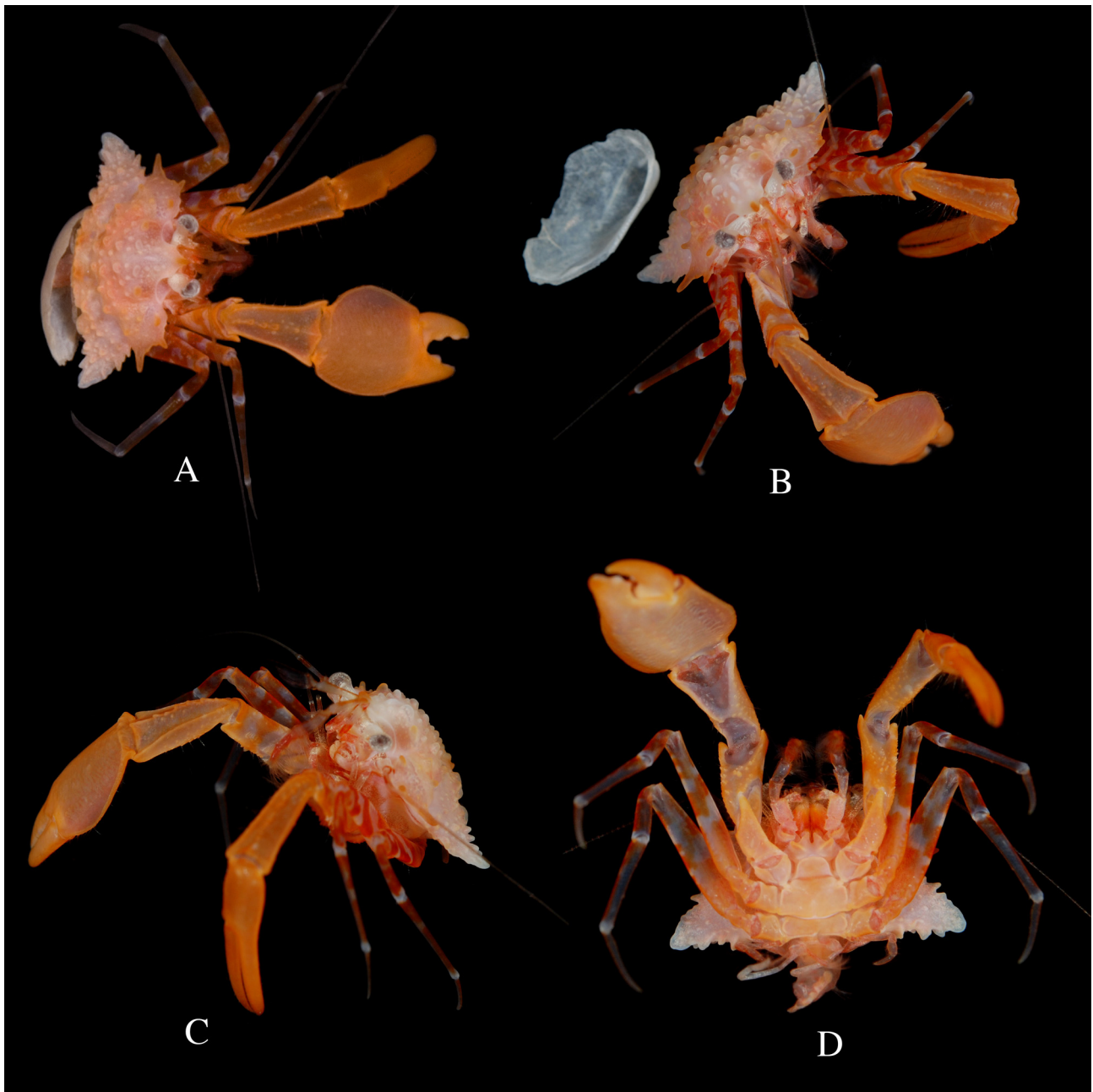

FIGURE 6. *Patagurus rex* **gen. & sp. nov.**, holotype male (UF 23548), habitus and coloration: A, anterodorsal view, carrying bivalve shell *Gregariella* sp., immediately after capture; B, frontal view, shell detached; C, anterolateral view, pleon not visible; D, ventral view, pleon exposed. Photographs: Gustav Paulay (A), Arthur Anker (B–D).

Discussion

Carcinization appears to be an advantageous strategy given the number of times it has occurred within the Decapoda and the ecological success and diversity of crab lineages (Bracken-Grissom *et al.* 2013). While brachyurans are by definition fully-carcinized decapods, anomurans show remarkably varied intermediate stages toward carcinization (Figs. 7, 8). Partly carcinized forms include the deep-sea squat-lobsters *Shinkaia* and *Kiwa* and the freshwater Aeglidae (Fig. 7J). Porcelain crabs (Porcellanidae, Fig. 7C) and the monotypic Lomisidae (*Lomis hirta* (Lamarck, 1818), Fig. 7B) display a more crab-like body form. Peculiar, fossorial crab-like forms evolved in the Hippoidea (Blepharipodidae, Hippidae, Lepidopidae, Fig. 7A). Other cases of anomuran carcinization have evolved directly from asymmetrical hermit crabs (Table 1), including lithodids, the fourth lineage of fully carcinized anomurans (Bracken-Grissom *et al.* 2013). Carcinization in hermit crabs is more complex than in other decapods. While carcinization in other Anomura involved predominantly broadening of the cephalothorax and reduction and underfolding of the pleon, in paguroids this process also implied reorganization and sclerotization of the cephalothorax and pleon as these animals abandoned using domiciles.

Seven groups of paguroids show tendencies toward carcinization (Table 1), involving reduction or armoring of the pleon, tendency to loose domiciles, and sclerotization of cephalothorax. In four groups, (1) *Probeebei* + *Tylaspis*, (2) *Bivalvopagurus,* (3) *Birgus*, and (4) *Tisea*, carcinization clearly occurred independently as these carcinized representatives originated in different families. The presumably closely related, deep-sea (>1000 m) parapagurids *Probeebei mirabilis* Boone, 1926 and *Tylaspis anomala* Henderson, 1885 appear to no longer live in shells, although *T. anomala* is known to hold anemones for protection (Wolff 1961; Lemaitre 1998). Both *Probeebei* and *Tylaspis* are characterized by enlarged, calcified carapaces, as well as fairly large pleons, largely sclerotized in *Probeebei*, but not in *Tylaspis*. The parapagurid *Bivalvopagurus sinensis* (de Saint Laurent, 1972) holds a bivalve shell over its abdomen together with an anemone that is attached to it, but has a largely calcified carapace. The coenobitid robber crab, *Birgus latro* (Linnaeus, 1767), the largest living terrestrial arthropod, only wears shells as a juvenile, and has a heavily sclerotized cephalothorax and pleon (Fig. 7I). The diogenid *Tisea grandis* Morgan & Forest, 1991*,* a large, deep-water (~250 m) hermit crab, is thought to carry a shell only over its well-developed pleon as the cephalothorax is large and fully sclerotized. *Tisea* is thought to be related to the shallow-water, large-bodied genera *Dardanus* and *Petrochirus* (Morgan & Forest 1991).

The remaining three groups, viz. (5) *Labidochirus* (Fig. 8A), (6) *Alainopagurus* + *Ostraconotus* + *Solitariopagurus* (Fig. 8D–G) + *Porcellanopagurus* (Fig. 8B,C) + *Patagurus* (Figs. 5, 6), and (7) Lithodidae (Fig. 7D–H), appear to be relatively closely related within the paraphyletic Paguridae (Bracken-Grissom *et al.* 2013). The two species of the pagurid genus *Labidochirus* wear small gastropod shells that typically cover only their abdomen, while the cephalothorax remains exposed and is sclerotized (Fig. 8A). *Labidochirus splendescens* (Owen, 1839) is regularly associated with the hydroid *Hydractinia serrata* Kramp, 1943, that covers and extends its gastropod domicile (Abrams *et al.* 1986). This hydroid carcinoecium is reminiscent of carcinoecia formed by actinians and zoanthids in some deep-water Parapaguridae (Fautin Dunn *et al.* 1980; Lemaitre 1996; Williams & McDermott 2004).

The pagurid genera *Ostraconotus*, *Alainopagurus, Solitariopagurus, Porcellanopagurus* and *Patagurus* appear to be related (Lemaitre & McLaughlin 1995; Poupin & McLaughlin 1996; McLaughlin 2000; present study). Members of these five genera also share (where known) the habit of wearing bivalve (or limpet) shells (Figs. 6A, 8B, F) over moderately developed to small pleons. They present various levels of calcification of the posterior carapace and tend to have a well-developed rostrum (Table 1; see below).

King crabs are the most crab-like anomurans, with fully calcified cephalothoraxes and leathery to calcified, under-tucked pleons. Molecular and combined molecular and morphological phylogenetic analyses recovered lithodids as a lineage derived from within pagurids, close to a group of northern temperate taxa, including *Pagurus*, *Labidochirus* and *Discorsopagurus* (Ahyong *et al.* 2009, Schnabel *et al.* 2011, Tsang *et al.* 2011, Bracken-Grissom *et al.* 2013), although until recently the pagurid origin of the Lithodidae was vividly debated (e.g., McLaughlin *et al.* 2004, 2007; Lemaitre & McLaughlin 2009).

TABLE 1.

Genus	Family	Domicile	Posterior carapace	Carapace length (L) to width (W)	Rostrum
Probeebei	Parapaguridae	no or unknown	calcified	L>W	well developed
Tylaspis	Parapaguridae	no, carries sea anemones	calcified	L>W	well developed
Bivalvopagurus	Parapaguridae	bivalve shell	calcified	L>W	moderately developed
Tisea	Diogenidae	gastropod shell?	calcified	L>W	poorly developed
Birgus	Coenobitidae	no (adults)	calcified	L>W	moderately developed
Labidochirus	Paguridae	small gastropod shell extended by *Hydractinia*	calcified	L>W	moderately developed
Ostraconotus	Paguridae	unknown	calcified	L>W	poorly developed
Alainopagurus	Paguridae	bivalve shell	membranous	L>W	moderately developed
Solitariopagurus	Paguridae	bivalve shell	membranous	L>W	well developed
Porcellanopagurus	Paguridae	bivalve or limpet shell	membranous	L>W	well developed
Patagurus	Paguridae	bivalve shell	calcified	W>L	well developed
Placetron, Hapalogaster etc.	Lithodidae Hapalogastrinae	no	calcified	W=L	well developed
Lithodes, Paralomis, Paralithodes, Lopholithodes etc.	Lithodidae Lithodinae	no	calcified	W>L or L>W	well to poorly developed

TABLE 1. (Continued)

Genus	Branchiostegites	Thoracic sternum	Pleon calcification	Pleon size	Depth range
Probeebei	calcified	normal	yes	large	1145–4775 m
Tylaspis	uncalcified	normal	no	large	3680–4344 m
Bivalvopagurus	unknown	normal	no	moderate	415–510 m
Tisea	calcified?	normal	no	large	220 m
Birgus	calcified	broad, tightly joined through sternite VI	yes	large	terrestrial
Labidochirus	uncalcified	normal	no	moderate	subtidal to ~ 400 m
Ostraconotus	unknown	unknown	no	small	214–230 m
Alainopagurus	partly calcified	broad	no	moderate	455–700 m
Solitariopagurus	uncalcified	broad, tightly joined through sternite VII	no	moderate	10–1400 m
Porcellanopagurus	uncalcified?	normal	no	moderate	5–500 m
Patagurus	calcified	broad, tightly joined through sternite VII	no	small	400 m
Placetron, Hapalogaster etc.	calcified?	broad, tightly joined through sternite VII	no (or weak)	moderate	intertidal to ~100 m
Lithodes, Paralomis, Paralithodes, Lopholithodes etc.	calcified	broad, tightly joined through sternite VII	yes	small to moderate	intertidal to deep-sea (3200 m)

FIGURE 7. Examples of carcinization in Anomura other than Paguridae: A, *Emerita portoricensis* Schmitt [Hippidae] from Rio Grande do Norte, Brazil; B, *Lomis hirta* (Lamarck) [Lomisidae] from South Australia; C, *Petrolisthes violaceus* (Guérin) [Porcellanidae] from Coquimbo, Chile; D, *Oedignathus inermis* (Stimpson) [Lithodidae, Hapalogastrinae] from Washington, USA; E, *Placetron wosnessenskii* Schalfeew [Lithodidae, Hapalogastrinae] from Washington, USA; F, *Phyllolithodes papillosus* Brandt [Lithodidae, Lithodinae] from Washington, USA; G, *Lithodes santolla* (Molina) [Lithodidae, Lithodinae] from Chile, dried specimen in a museum exhibit; H, *Cryptolithodes typicus* Brandt [Lithodidae, Lithodinae] from Washington, USA; I, *Birgus latro* (Linnaeus) [Coenobitidae] from Guam; J, *Aegla* sp. [Aeglidae], aquarium specimen imported from southern South America. Photographs: Arthur Anker (A, C, G, I, J), Michael Marmach (B), Gustav Paulay (D–F, H).
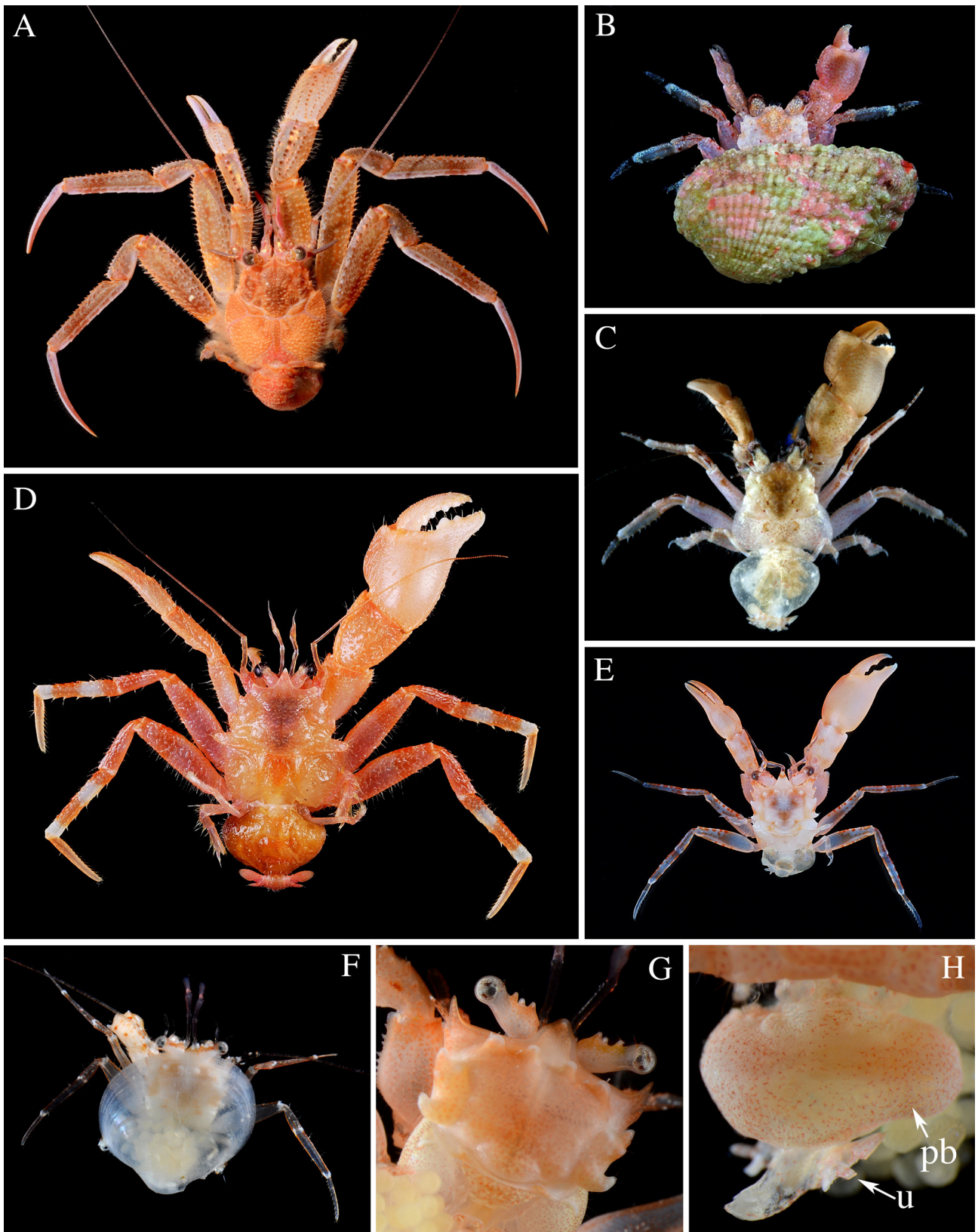
FIGURE 8. Examples of carcinized Paguridae: A, *Labidochirus splendescens* (Owen) from Washington, USA; B, C, *Porcellanopagurus truncatifrons* Takeda from Kume-jima (B) and Okinawa (C), Japan, with (B) and without (C) shell; D, *Porcellanopagurus filholi* de Saint Laurent & McLaughlin from Panglao, Philippines; E, *Solitariopagurus tuerkayi* McLaughlin from Kume-jima, Japan; F, G, H, *Solitariopagurus trullirostris* McLaughlin from Moorea, French Polynesia, individual with shell (F), details of carapace (G), and pleon (H), arrows indicating ventral pleonal bulge (pb) and left uropod (u). Photographic credits: Gustav Paulay (A, F, G, H), Tin-Yam Chan (B, D, E), Tohru Naruse (C).

Morphological changes. The functional morphological changes involved in carcinization of hermit crabs include numerous modifications that are best examined by body region, viz. cephalothorax, pleon, chelipeds, and posterior (fourth and fifth) pereopods.

(1) The cephalothorax becomes sclerotized, box-like, with rigid articulation or fusion of sclerotized elements. This involves (a) sclerotization and tight articulation/fusion of carapace regions, including the posterior carapace and branchiostegites (normally membranous in paguroids), to form a more or less rigid carapace, often with ornamentation on the dorsal surface and anterior (rostral) and anterolateral margins; (b) fusion of the cephalic sternal elements (e.g. epistome) with the carapace; (c) broadening, calcification and ultimately fusion of sternites; and (d) tight articulation between the ventral margin of the branchiostegites and the underlying thorax.

Patagurus approaches brachyurans and lithodids in the level of carapace widening, sclerotization, and fusion of the cephalothorax more than any other member of the Paguridae. The carapace is substantially wider than long, proportionately broader than in any other pagurid, and fused into a single dorsal element, with only a narrow, posterior membranous band remaining non-calcified. The carapace is also more ornamented than in other pagurids, with large lateral projections, teeth and tubercles all over the dorsal surface as well as on the anterolateral and lateral margins. The epistome is fused into a single plate incorporating at least the interocular plate, antennal sternites, and lateral elements that remain separated in typical pagurids; this plate remains delineated from the carapace by a suture running along its anterior and anterolateral margins. The branchiostegites are calcified along their dorsal margin and tightly articulated with the dorsal carapace, but remain membranous along their ventral margin. Sternites III–VII are tightly articulated (immovable relative to each other, but with sutures clearly visible), forming a single, broad structure, as in the closely related *Solitariopagurus* and the more distant king crabs.

(2) The pleon is reduced, tucked under the cephalothorax, and calcified. The pleon undergoes drastic transformation across the Decapoda. In basal decapods (and eumalacostracans in general), the pleon is an organ devoted to locomotion (Hessler 1983), with hypertrophied musculature displacing viscera (gonads and digestive glands). In some demersal and fossorial groups (e.g., some alpheids, axiideans, stomatopods) and in some symbiotic crabs (pinnotherids, cryptochirids) that live in a protected environment, the gonads are extended into at least the anterior abdominal somites. Hermit crabs have carried this process to the extreme, extending their gonad and digestive gland so that these organs dominate the mass of the pleon, whilst reducing the musculature and abandoning pleonal locomotion. Carcinized hermit crabs have generally retained viscera in their pleon making reduction and underfolding challenging. Thus *Probeebei* and *Birgus* retain large, but heavily sclerotized pleons (Fig. 7I). In all lithodids examined for this study (*Hapalogaster mertensii* Brandt, 1850 (UF 37939), *Oedignathus inermis* (Stimpson, 1860) (UF 34570), *Placetron wosnessenskii* Schalfeew, 1892 (UF 31225), *Cryptolithodes typicus* Brandt, 1848 (UF 34553), *Phyllolithodes papillosus* Brandt, 1848 (UF 34564), *Lopholithodes mandtii* Brandt, 1848 (UF 37938), *Rhinolithodes wosnessenskii* Brandt, 1848 (UF 37940)), the pleon is quite spacious, dorso-ventrally thickened, accommodated in a broad concavity over the sternum, and contains large extensions of the digestive gland. To our best knowledge, this important feature has not been previously reported and represents additional evidence for the derivation of king crabs from hermit crabs. This is in marked contrast with the transformation of the pleon from shrimp or squat lobster forms to porcellanid and true crabs, where the viscera remain within the cephalothorax, the musculature is atrophied, and the associated locomotory behaviors (tail flip escape) are eventually lost (in brachyurans).

The pleon of *Patagurus* and putatively related pagurid genera is small and non-sclerotized. The pleon is no longer held within a domicile; rather a shallow, dish-like shell is held over the body (e.g., in *Solitariopagurus*, Fig. 8F) or only over the greatly shortened pleon (in *Patagurus*, Figs. 4C, 6A). Although the pleon of the single male holotype of *Patagurus rex* was not dissected, it appears to have little room for viscera. Females in *Solitariopagurus* have a similarly short and narrow "core" to their pleon. However a broad, pillow-like bulge extends ventrally from the pleon (Fig. 8H), which appears to be loaded with oocytes, thus permitting the animal to retain a substantial mass of viscera in an otherwise shortened pleon.

(3) The chelipeds of carcinized anomurans are typically held folded laterally (Fig. 7B–E), parallel to the front, rather than extended anteriorly (as in squat lobsters) or folded ventrally (as in most paguroid lineages). Repositioning of chelipeds is marked in most Brachyura, Porcellanidae, Lomisidae, Lithodidae, but most paguroids, including *Patagurus*, retain ventrally folded claws. Noteworthy, the dactylus is typically in dorsolateral ("outer") to dorsal position in most brachyuran claws, but usually in mesial ("inner") position in anomuran crabs, including porcellanids, lomisids, lithodids, and many paguroids.

(4) The fourth and fifth pereopods of most anomurans are reduced and may be simple, subchelate, or chelate (Tudge *et al.* 2012). In paguroids, the propodi of the last two pairs usually bear broad rasps that are used to hold on to the shell via friction. Propodal rasps tend to be reduced or lost in carcinized lineages coincident with the abandonment of gastropod domiciles, although remnants are still present in some, even in lithodids (Richter & Scholtz 1994). *Patagurus* and *Solitariopagurus* have transformed the propodal rasp on the fourth pereopod into a single row of sharp spines, and while a rasp is still visible on the propodus of the fifth pereopod in *Solitariopagurus*, it is not discernible in *Patagurus*. These changes appear to relate to carrying rather than wearing domiciles, and the fourth pereopod somewhat resembles that of various carrier crabs, such as homolids and dromiids. The thoracic sternum of *Solitariopagurus* and *Patagurus* is further convergent to the sternum in those brachyurans groups in turning upward (dorsally) at its posterior (sternites VII & VIII), so that the fourth and fifth pereopods arise in a dorsal to anterodorsal position over the third pereopods.

Pathways to carcinization. Tendencies toward carcinization in paguroids involve reducing/losing the domicile. Alternative strategies in paguroids appear to rely on armor vs. speed for protection. For example, most diogenids associated with coral reefs (e.g., *Aniculus, Calcinus, Clibanarius, Dardanus*), the terrestrial *Coenobita*, as well as many temperate and subtropical pagurids (e.g., *Pagurus, Petrochirus*) rely on fully withdrawing into large, thick shells. They tend to possess enlarged, heavily calcified, and sometimes armed (with tubercles, spines, dense setae) chelipeds and walking legs for protection; many can use their chelipeds and sometimes second pereopods as opercula. Several species also carry sea anemones on their shells for even more protection (Williams & McDermott 2004). In contrast, other hermit crabs, such as most pagurids on coral reefs (e.g., *Catapagurus, Pagurixus, Trichopagurus*) rely on speed, tend to have long legs, and inhabit relatively small shells into which they often cannot fully withdraw. Carcinized paguroids likely originated from ancestors that relied on speed rather than armor for protection. The temperate pagurid *Labidochirus splendescens* provides a good model of this trend, with long powerful ambulatory legs (Fig. 8A), rapid locomotion, wearing small and light shells that generally accommodate only the pleon. These fast and light animals also have a tendency to abandon even their small shell when fleeing. The sclerotization of the cephalothorax in *Labidochirus* makes adaptive sense in light of lack of protection from their domicile, as it does in other carcinized hermit crabs that have reduced or no domiciles. In fact, an innate tendency towards sclerotization of the cephalothorax is evident in hermit crabs that are kept without access to domiciles (Przibram 1907; Harvey 1998; Reimann *et al.* 2011). *Patagurus* also fits this general tendency: although having a relatively well-sclerotized shield, this remarkable hermit crab nevertheless has long ambulatory legs for rapid movement.

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