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A new genus for four species of hermit crabs formerly assigned to the genus *Pagurus* Fabricius (Decapoda: Anomura: Paguridae)

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Abstract.—A new genus, *Propagurus*, is described for four species formerly assigned to the hermit crab genus *Pagurus* Fabricius. The species, all very *Pagurus*-like in overall appearance, are characterized by having gills of a quadriserial nature and rudimentary pleurobranchs on the fifth and sixth thoracic somites (above the second and third pereopods).

During a review of South African species assigned to the hermit crab genus *Pagurus* Fabricius, 1775 (McLaughlin & Forest 1998), the holotype of *Pagurus deprofundis* (Stebbing 1924) was reexamined for the first time. Two characters immediately set Stebbing's species apart from other members of the genus, i.e., its asymmetrical, quadriserial gill structure, and a longitudinal keel on the mesial face of the propodus of each second pereopod. The general body morphology and telson structure reminded one of the authors (JF) of the South American *Pagurus gaudichaudii* H. Milne Edwards, 1836. In a report by Forest & de Saint Laurent (1968) on species of *Pagurus* collected during the voyage of the *Calypso* to the Atlantic coast of South America, these authors established four distinct species groups for South American species within this heterogeneous genus. *Pagurus gaudichaudii* (as *P. gaudichaudi*) was recognized as distinct from all other described *Pagurus* species and assigned to a monotypic group ("groupe *gaudichaudi*"), characterized by having rudimentary pleurobranchs on the fifth and sixth thoracic somites (above the second and third pereopods) and a quadriserial gill structure. When *P. deprofundis* was closely examined, it too was found to have pleurobranchs on the fifth and sixth thoracic somites; however, in Stebbing's (1924) unique specimen, only the pleurobranch of the sixth thoracic somite was rudimentary; that of the fifth was moderately well developed.

At the time the *gaudichaudi* group was established, Forest & de Saint Laurent (1968) indicated that they had examined several Indo-Pacific specimens, then still unidentified, that shared the gill number and structure of *P. gaudichaudii*, but differed from the South American species in several important characters. They considered that *P. gaudichaudii* was probably an unique species for which a new genus should be considered. We have now reexamined the referred-to Indo-Pacific specimens and have found most to represent *P. deprofundis* that had previously gone unrecognized because of Stebbing's (1924) inadequate and inaccurate original description and figures.

When McLaughlin (1997) described *Pagurus haigae* from the French-Indonesian KARUBAR expedition to Indonesia, she failed to detect the quadriserial nature of the gills in that species, or the presence of rudimentary pleurobranchs on the fifth and sixth thoracic somites. Like *P. gaudichaudii*, *P. haigae* lacks the propodal keel of *P. deprofundis*. A few of the Indo-Pacific specimens examined earlier by Forest & de

Saint Laurent also proved to be conspecific with *P. haigae*. McLaughlin (1997) contrasted *P. haigae* with *P. yokoyai* Makarov, 1938 and *P. brachiomastus* (Thallwitz 1892). Reexamination of specimens of these latter two species has shown that *P. yokoyai*, but not *P. brachiomastus*, has the same gill structure and number as the above mentioned taxa. For these four species we now propose a new genus. It must be noted that *Pagurus* remains a very heterogeneous taxon. As better knowledge of the species currently assigned to *Pagurus* becomes available, there will certainly be further apportionment.

With the exception of one specimen in the personal collection of one of the authors (PMcL), materials for this study have come from the following institutions: Museums and Art Galleries of the Northern Territories, Darwin, Australia (NTM), Muséum national d'Histoire naturelle, Paris, France (MNHN), Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand (NMNZ) (formerly the National Museum of New Zealand), Museum of Victoria, Melbourne, Australia (NMV), National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. (USNM), Natural History Museum and Institute, Chiba, Japan (CBM-ZC), New Zealand Oceanographic Institute, Wellington, New Zealand (NZOI) (now part of the National Institute of Water and Atmospheric Research), Osaka Museum of Natural History, Osaka, Japan (OMNH), Swedish Natural History Museum, Stockholm, Sweden (SNHM), The Natural History Museum, London, U.K. (NHM), and Zoological Museum, University of Copenhagen, Denmark (ZMUC). These specimens have been returned to their institutions of origin. Shield length (sl), measured from the tip of the rostrum or midpoint of the rostral lobe to the midpoint of the posterior margin of the shield, or carapace length (cl), measured from the tip of the rostrum or midpoint of the rostral lobe to the midpoint of the posterior margin of the carapace provides an indication of animal size. The abbreviation ovig. indicates ovigerous female. The following abbreviations indentify campaignes, expeditions, vessels, sample type, or gear: SMIB, Substances Marines d'Intérêt Biologique; KARUBAR, acronym for the French-Indonesian campaign to the Islands of Kai, Aru and Tanimbar; MUSORSTOM, acronym for the joint expeditions by the Muséum national d'Histoire naturelle, Paris, and Office de la Recherche Scientifique et Technique Outre-Mer; FR, Fisheries Research; CM, *Chiyo Maru*; JO, *James Cook*; SM, *Shinkai Maru*; So, *Soela*; BS, bottom sample; DW, Warén dredge; CP, beam trawl; CC, shrimp trawl.

Propagurus, new genus

Eupagurus.—Barnard, 1950:458 (in part); not *Eupagurus* Brandt, 1851.

Pagurus.—Makarov, 1938:169; 1962: 181 (in part).—Miyake, 1978:78 (in part).—McLaughlin, 1997:525 (in part); not *Pagurus* Fabricius, 1775.

Type species.—*Pagurus gaudichaudii* H. Milne Edwards, 1836.

Diagnosis.—Thirteen pairs of symmetrical or asymmetrical, generally quadriserial gills (Fig. 1): 2 arthrobranchs on each third maxilliped, cheliped and second through fourth pereopods; single moderately well developed or rudimentary pleurobranch on fifth thoracic somite, rudimentary pleurobranch on sixth thoracic somite, and well developed pleurobranch on seventh thoracic somite (above fourth pereopod). Ocular acicles subacutely to roundly triangular. Basal segment of antennular peduncle with strong lateral spine (Fig. 2A). Antennal peduncles with laterodistal projection of second segment well developed, mesial margin spinose. Maxillule (Fig. 2B–E)) with external lobe of endopod varying from vestigial or rudimentary to well developed, arched, but not strongly recurved. Third maxilliped (Fig. 2F, G) with basis-ischium fusion incomplete; crista dentata well developed and with strong accessory tooth. Sternite of

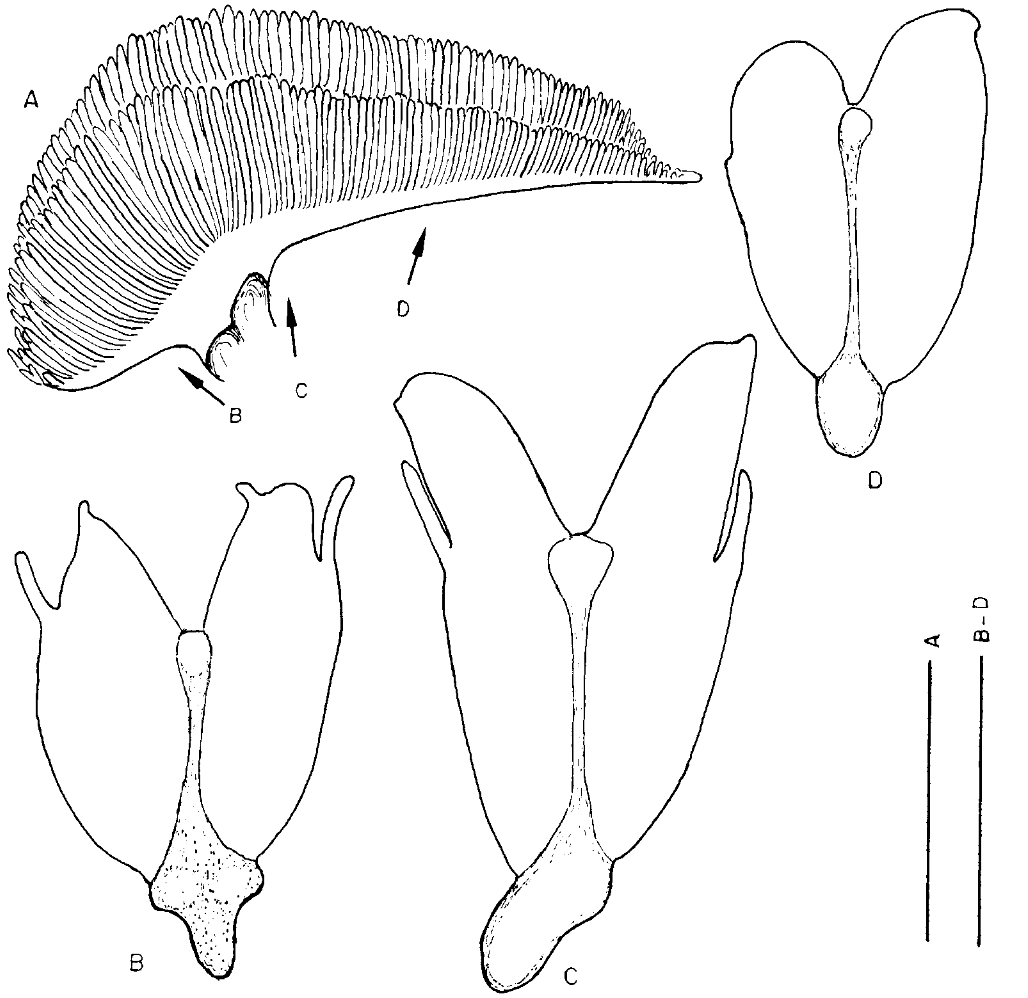

Fig. 1. Right anterior arthrobranch of third pereopod of *Propagurus gaudichaudii* (H. Milne Edwards, 1836), new combination, ♂ (cl = 21 mm) MNHN-Pg 2550. A, entire gill; B–D, sections at indicated levels showing lamellar shapes. Scales equal 2 mm (B–D) and 5 mm (A).

third maxillipeds (third thoracic sternite) with spine on each side of median concavity. Left second and third pereopods shorter than right; propodus and dactyl of left third with more prominent setation. Fourth pereopods with propodal rasp consisting of 2 to several rows of corneous scales. Eight thoracic sternite (sternite of fifth pereopods) (Fig. 3A) with broadly and ovately subrectangular lobes, each with horizontal or transverse tuft of long setae.

Abdomen well developed, somites often delineated dorsally by strong transverse fibrils; tergite of sixth somite strongly calcified, with deep submedian transverse furrow dividing tergite into subquadrate anterior and subrectangular posterior lobes. Uropods markedly asymmetrical. Telson with deep submedian transverse indentation providing indication of division into anterior and posterior portions; asymmetrical posterior lobes separated by median cleft.

Males with paired gonopores, each partially masked by adjacent tuft of stiff setae; no sexual tubes; no paired pleopods, usually three unpaired left pleopods, third (Fig. 3B)

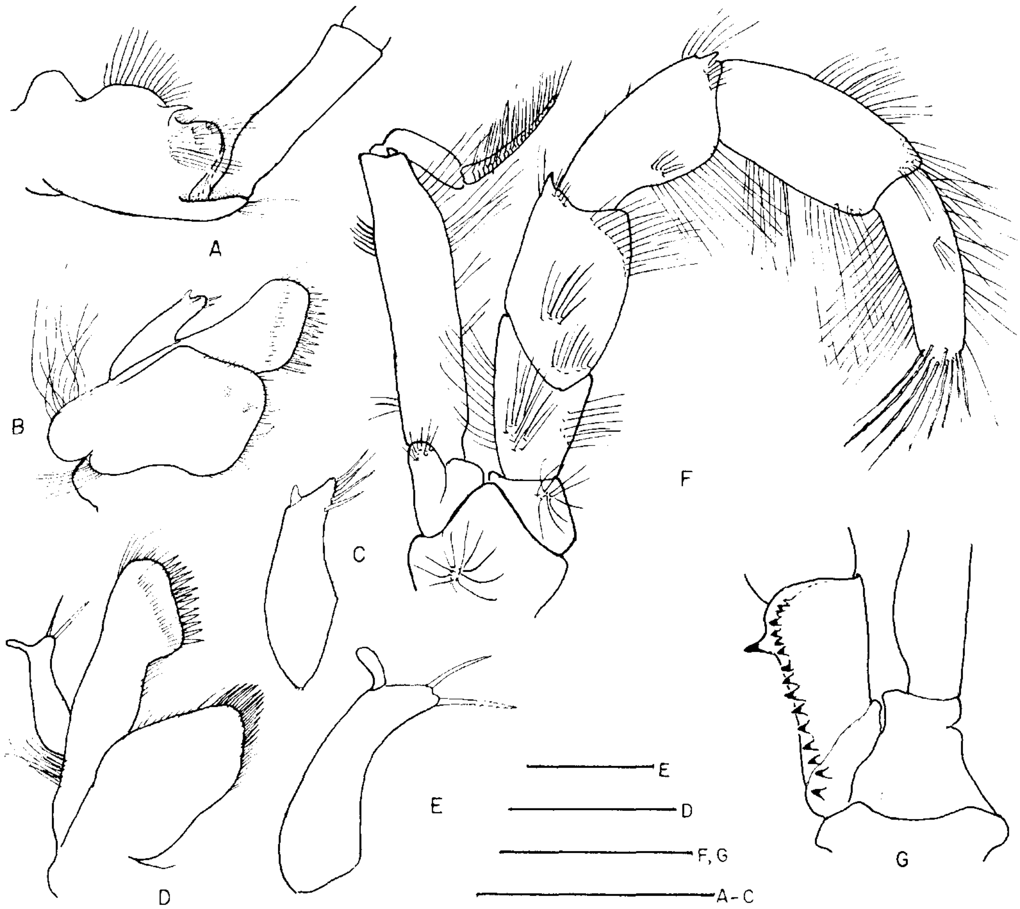

Fig. 2. Cephalic appendages. A–C, F, G, *Propagurus gaudichaudii* (H. Milne Edwards, 1836), new combination, ♂ (cl 21 = mm), MNHN-Pg 2550; D, E, *Propagurus deprofundis* (Stebbing, 1924), n. comb, ♂ (sl = 11.2 mm), NZOI sta. E719: A, antennule (lateral view); B, D, maxillule (lateral view); C, E, endopod of maxillule, enlarged; F, third maxilliped, lateral view; G, basis-ischium of third maxilliped showing development of crista dentata. Scales equal 1 mm (E), 2 mm (D), and 5 mm (A–C, F, G).

to fifth each with somewhat foliaceous elongate endopod and rudimentary exopod. Females with paired gonopores; no paired pleopods, 4 unpaired left pleopods, second (Fig. 3C) with subequal rami, both short, somewhat paddle-shaped, third (Fig. 3D) and fourth each with elongate somewhat foliaceous endopod and short paddle or blade-shaped exopod; fifth as in male.

Etymology.—From the Greek *pro* meaning before, and *pagouros* meaning crab and referring to the more primitive characters of this very *Pagurus*-appearing genus. Genus masculine.

Remarks.—We have chosen to use the term "quadriserial" in reference to gill structure equivalent to Lemaitre's (1989) trichobranchiate and intermediate conditions. Studies by one of us (MST) have shown that it is not the shape of the gill elements, so much as their insertion on the rachis of the gill that determines the gill type. In true trichobranchiate gills the tubular elements are equal or unequal, but inserted in order or disorder, around the axis, or in regular transverse rows along the axis. In contrast, the elements of phyllobranchiate gills almost always are inserted biserially

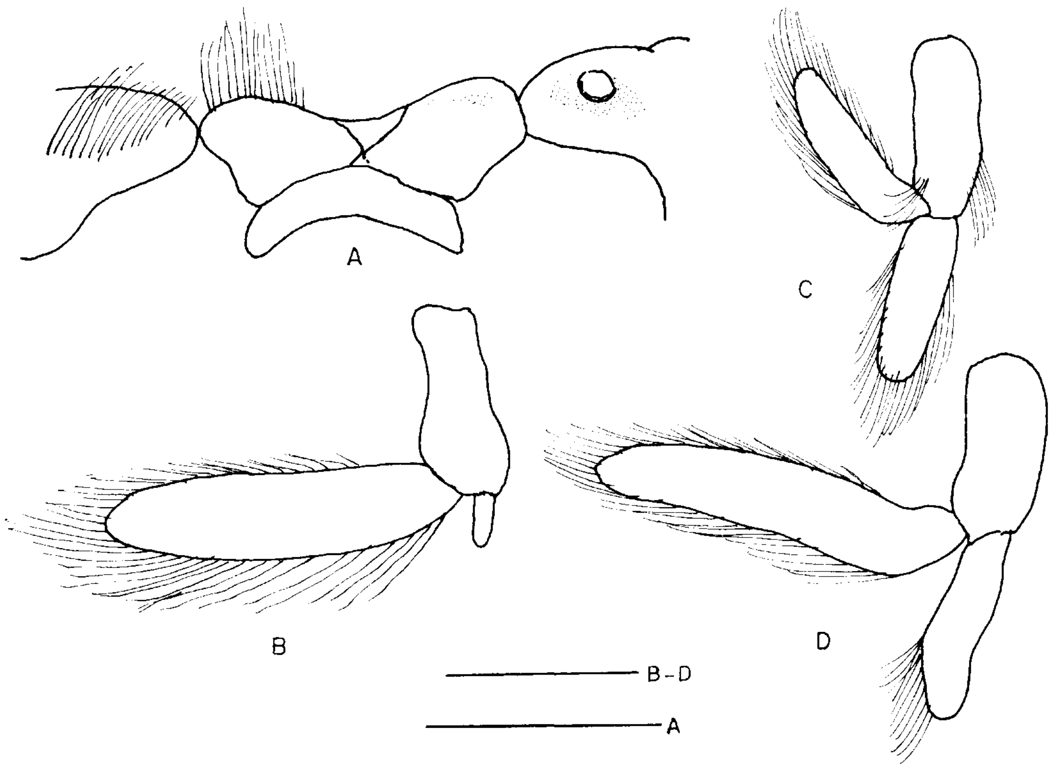

Fig. 3. *Propagurus gaudichaudii* (H. Milne Edwards, 1836), new combination. A, ♂ (cl = 25 mm), MNHN-Pg 2550; B, ♂ syntype (sl = 18.6 mm) of *P. patagoniensis* (Benedict, 1892), USNM 16772; C, D, ♀ syntype (sl = 16.0 mm) of *P. patagoniensis* (Benedict, 1892), USNM 16772. A, sternite and coxae of fifth pereopods (ventral view, setae omitted from left side); B, C, second left pleopod; D, third left pleopod. Scales equal 5 mm.

in regular pairs along the rachis. There are many types of true trichobranch gills, just as there are phyllobranch gills. The quadriserial appearing gills of *Propagurus*, like those of pylochelids and some parapagurids, are inserted biserially on the rachis; it is the lamella of each pair that is divided, equally or unequally, giving a "trichobranch" or "intermediate" appearance. However, as may be seen in Fig. 1, the lamellar structure varies from one level of the rachis to another. Similarly, the degree of asymmetry may vary from one arthrobranch to another.

In certain morphological characters, species of *Propagurus* seems to be undergoing evolutionary transformations from those seen in the typical *Pylopaguropsis* group of pagurid genera (cf. de Saint Laurent-Dechancé 1966) to those seen in *Pagurus*-like genera. Three important variations seen among the species of this new genus offer support to this hypothesis: the overall development of the gill lamellae, which varies, even within a single species from deeply quadriserial to only weakly so; reduction of the pleurobranch of the fifth thoracic somite, which varies from moderately well developed to rudimentary; and development of the external endopodal lobe of the maxillule that is quite well developed in two species, rudimentary in another, and variable in the fourth.

A key to the species is provided, however exclusive reliance on it for species identifications is not recommended. Only in the case of *P. deprofundis* will a single character distinguish the species with certainty. Differentiation between *P. haigae* and *P. yokoyai* is particularly difficult, because of their considerable morphological similarities and magnitudes of intraspecific variation.

Key to the species of *Propagurus*, new genus

1. Left chela with dorsal surface uniformly covered with strong, tuberculate spines; dactyls of ambulatory legs each with only few distal strong spines on ventral margin, followed by row of tiny widely-spaced spinules; propodi of second pereopods each with dorsal row of corneous-tipped spines (southern South America) .... *P. gaudichaudii*, new combination
–. Left chela with distinct median row of spines, separating dorsal surface into strongly armed lateral portion and more tuberculate mesial portion; dactyls of ambulatory legs each with complete row of strong corneous spines on ventral margin; propodi of second pereopods without dorsal row of corneous-tipped spines 2
2. Propodi of second pereopods each with longitudinal keel on mesial face; lateral faces of palms of chelipeds each with few to several rows of closely-spaced tubercles or blunt spines (South Africa, southern Australia, New Zealand, Philippine and Hawaiian Islands) .... *P. deprofundis*, new combination
–. Propodi of second pereopods without longitudinal keel on mesial face; lateral faces of palms of chelipeds without few to several rows of closely-spaced tubercles or blunt spines 3
3. Distal margins of corneas usually not reaching to mid-length of fully extended ultimate segments of antennular peduncles; dorsomesial surface of palm of left cheliped with tufts of setae accompanied by several small spines; telson without, or with row of accessory spinules on dorsal surfaces adjacent to terminal margin (Indonesia, New Caledonia, Coral and Tasman Seas) .... *P. haigae*, new combination
–. Distal margins of corneas reaching to or beyond mid-length of fully extended ultimate segments of antennular peduncles; dorsomesial surface of palm of left cheliped with tufts of setae sometimes accompanied by low protuberances; telson with 2 to several rows of accessory spinules on dorsal surfaces adjacent to terminal margin (Japan) .... *P. yokoyai*, new combination

Propagurus gaudichaudii (H. Milne Edwards 1836), new combination

Figs. 1A–D, 2A–C,F,G, 3A–D, 4A, 5A–F, 6A–D, 7A, 11A, B

Pagurus Gaudichaudii H. Milne Edwards, 1836:269.—Nicolet, 1849:188.
Pagurus Gaudichaudi.—H. Milne Edwards, 1837:217.—Porter, 1935:137.
Bernhardus barbiger A. Milne Edwards, 1891:28, pl. 3, figs 1, 1a–c.
Eupagurus patagoniensis Benedict, 1892: 3.—Alcock, 1905:181 (list).–Barattini & Ureta, 1960:52, unnumbered fig.
Pagurus patagoniensis.—Benedict, 1901: 465, unnumbered fig.
Pagurus barbiger.—Benedict, 1901:466.—Rathbun, 1910:598.—Porter, 1935:137.
Eupagurus barbiger.—Lenz, 1902:737.—Lagerberg, 1905:4.—Alcock, 1905:180 (list).—Doflein & Balss, 1912:31.
Pagurus gaudichaudii.—Rathbun, 1910: 598.
Pagurus gaudichaudi.—Haig, 1955:24.—Gordan, 1956:330 (lit).—Forest & de Saint Laurent, 1968:142, fig. 112.—Scelzo & Boschi, 1973:208.—Scelzo, 1973: 166; 1976:43.—McLaughlin, 1974:43.—Boschi et al., 1981:244.—Boschi et al., 1992:53, fig. 51.

Holotype of *Pagurus gaudichaudii*.—♂ (sl = 13 mm), Valparaiso, MNHN Pg 221 (damaged).

Holotype of *Pagurus barbiger*.—♀ (sl = 6.9 mm), Orange Bay, Patagonia, 22 m, 29 Dec 1882, MNHN Pg 2401.

Syntypes of *Pagurus patagoniensis*.—1 ♂, 1 ♀ (sl = 15.5, 11.8 mm), *Albatross* sta. 2768, east coast of Patagonia, 79 m, 1888, USNM 16772.

Other material examined.—Argentina:

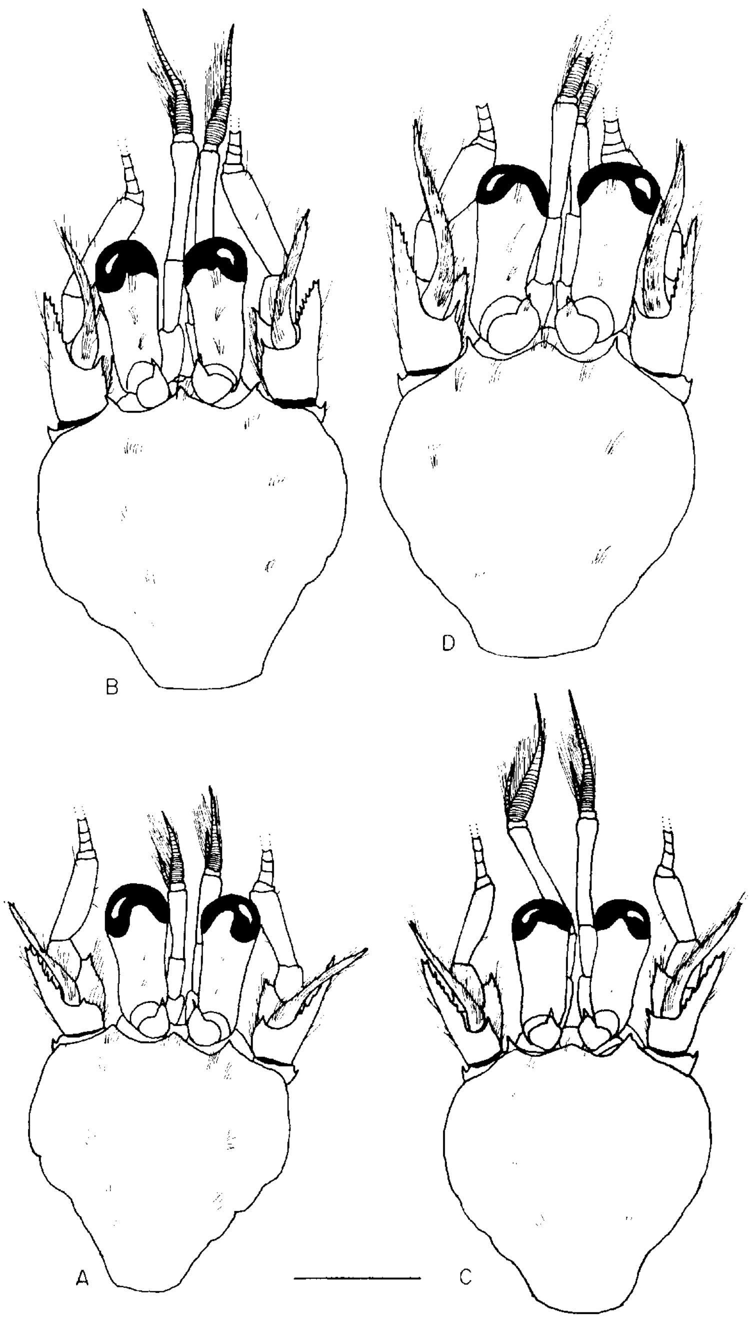

Fig. 4. Shield and cephalic appendages. A, *Propagurus gaudichaudii* (H. Milne Edwards, 1836) new combination, ♀ (sl = 16.0 mm), MNHN-Pg 2852; B, *Propagurus deprofundis* (Stebbing, 1924) new combination, ♂ (sl = 11.2 mm), NZOI; C, *Propagurus haigae* (McLaughlin, 1997) new combination, ♂ (sl = 17.1 mm) NTM Cr 6864; *Propagurus yokoyai* (Makarov, 1938) new combination, ♂ (sl = 11.5 mm), OMNH Ar 1941. Scale equal 5 mm (B, D) and 7.5 mm (A, C).

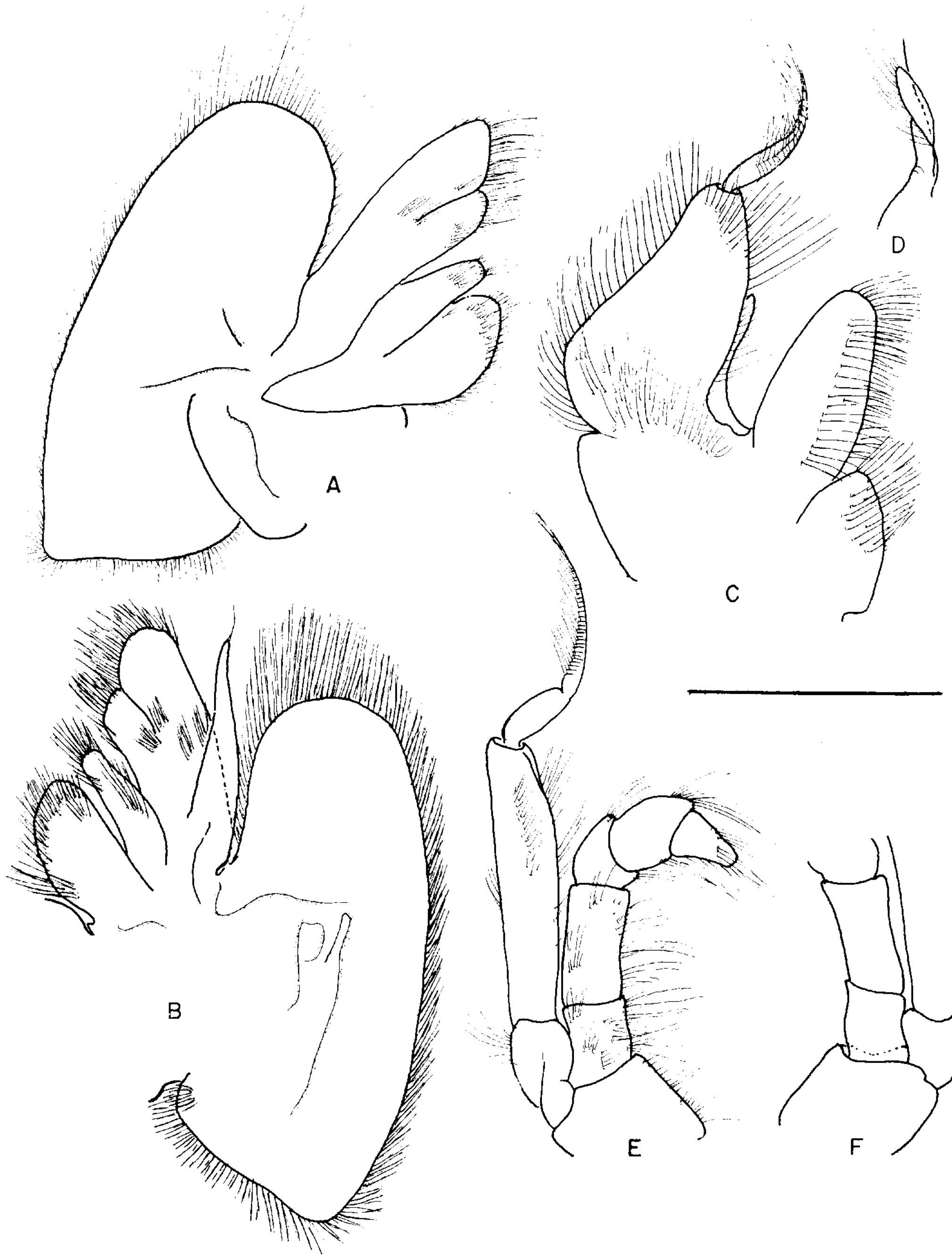

Fig. 5. *Propagurus gaudichaudii* (H. Milne Edwards, 1836), ♂ (cl = 21 mm), MNHN-Pg 2550, mouthparts. A, maxilla (lateral view); B, maxilla (mesial view); C, first maxilliped (lateral view); D, enlarged distal portion of endopod of first maxilliped; E, second maxilliped (lateral view); F, basis-ischium of second maxilliped (mesial view). Scale equals 5 mm.

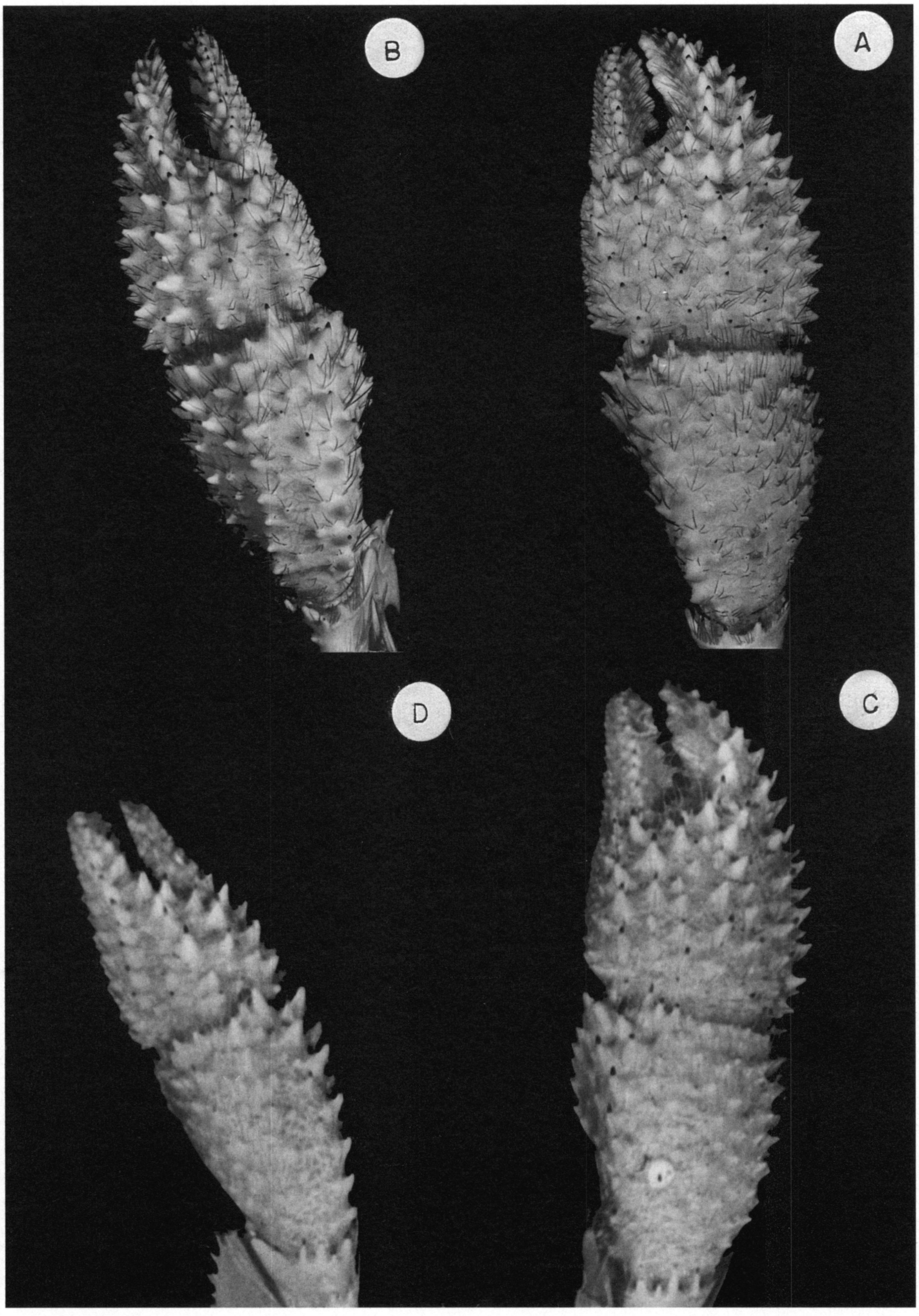

Fig. 6. *Propagurus gaudichaudii* (H. Milne Edwards, 1836) new combination. A, C, chela and carpus of right cheliped; B, D, chela and carpus of left cheliped. A, B, ♀ (sl = 16.0 mm), MNHN-Pg 2852; C, D, syntype of *Pagurus patagoniensis* (Benedict, 1982), ♀ (sl = 11.8 mm), USNM 16772. Magnifications equal 1.6× (A), 1.9× (B), 2.6× (C), and 2.1× (D).

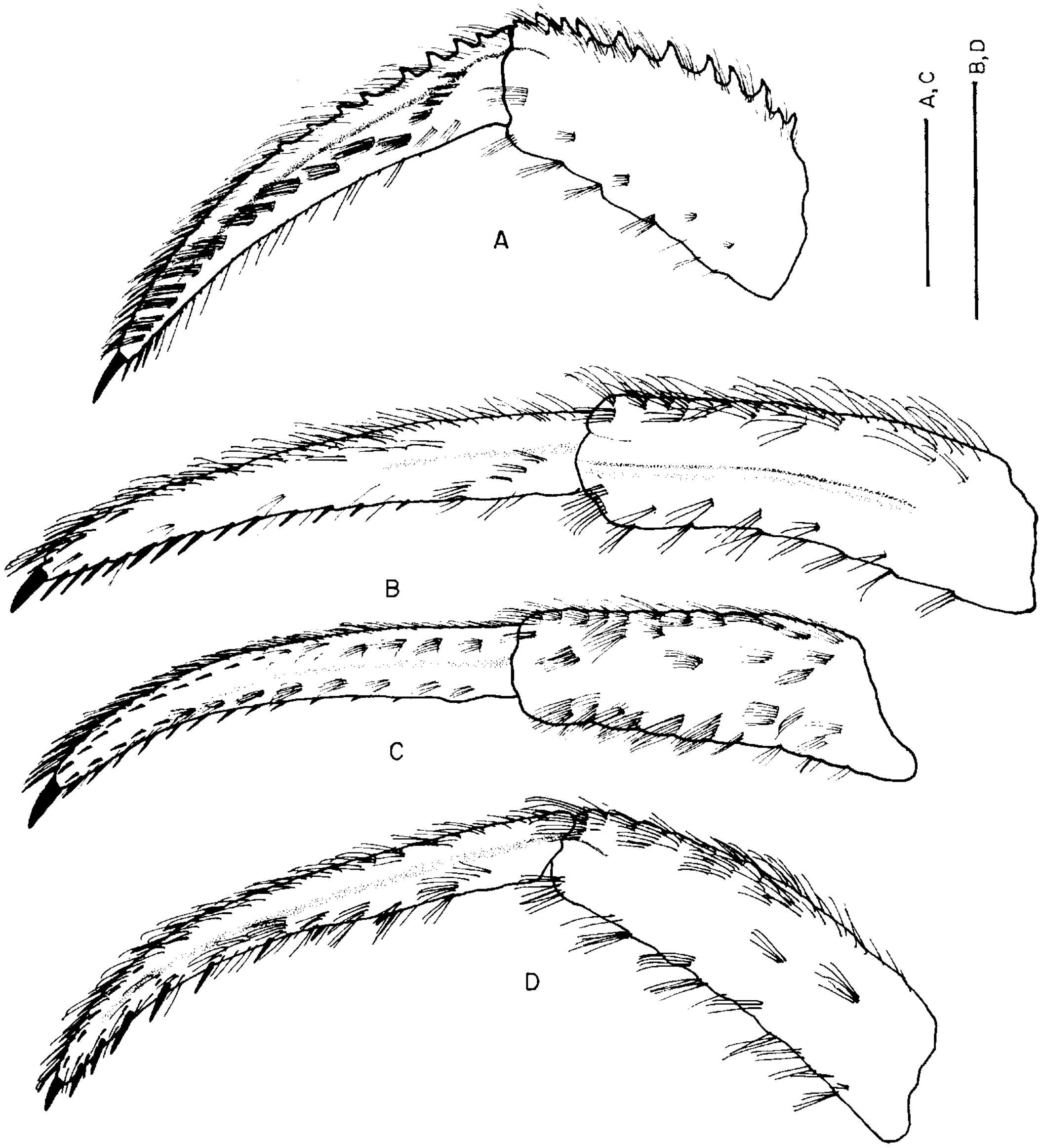

Fig. 7. Dactyl and propodus of second right pereopod (mesial view). A, *Propagurus gaudichaudii* (H. Milne Edwards, 1836) new combination, ♀ (sl = 16.0 mm), MNHN-Pg 2852; B, *Propagurus deprofundis* (Stebbing, 1924) new combination, ♂ (sl = 11.2 mm), NZOI; C, *Propagurus haigae* (McLaughlin, 1997) new combination, ♂ (sl = 17.1 mm) NTM Cr 6864; D, *Propagurus yokoyai* (Makarov, 1938) new combination, ♂ (sl = 11.5 mm), OMNH Ar 1941. Scales equal 5mm.

2♂ (cl = 33.0, 41.0 mm), 36°30′S, 54°00′W, 9 Jul 1961, coll. L. Rossi MNHN Pg 2550. *Calypso*, eastern South America (1961–1962): 4 ♂ (cl = 22.0–45.0 mm), 2 ovig. ♀ (cl = 27.0, 37.0 mm), sta. 169 off Rio de la Plata, 37°00′S, 55°21′W, 69 m, 29 Dec 1961, MNHN Pg 2852.—3 ♂ (cl = 41.0–48.0 mm), 1 ♀ (cl = 35.0 mm), sta. 170, 37°24.5′S, 54°56′W, 126–132 m, 9 Dec 1961, MNHN Pg 2851.—1 ♂ (cl = 37.0 mm), sta. 173, 38°25.54′S, 56°14′W, 81 m, 30 Dec 1961, MNHN Pg 2853.

Diagnosis.—Shield (Fig. 4A) varying from slightly broader than long to slightly longer than broad. Rostrum roundly subtriangular, subacute, sometimes produced beyond level of lateral projections; with or without terminal spine. Lateral projections broadly triangular or rounded, with or without submarginal spine. Ocular peduncles slightly more than half to approximately 0.75 length of shield; broader at base of corneas than proximally; corneas slightly dilated. Ocular acicles ovately or roundly triangular, dorsal surfaces somewhat concave, each with strong, sometimes corneous-tipped submarginal spine. Antennular peduncles overreach distal margins of corneas by 0.50–0.65 length of ultimate segment; basal segment with strong spine on lateral surface in distal half. Antennal peduncles overreach distal margins of corneas by 0.15–0.35 length of ultimate segment; second segment with laterodistal angle reaching to or beyond distal margin of fourth peduncular segment, with simple or bifid terminal spine, mesial margin with 4–7 corneous-tipped spines, lateral margin with few tufts of setae, dorsomesial distal angle with small corneous-tipped spine; first segment sometimes with spine on distolateral margin dorsally; ventrolateral margin with 1 small spine. Antennal acicles reaching to or beyond distal margins of corneas, each with strong terminal spine and numerous tufts of long stiff setae on mesial face.

External enopodal lobe of maxillule (Fig. 2B, C) rudimentary. Maxilla (Fig. 5A, B) with broad scaphognathite. First maxilliped (Fig. 5C, D) with short, distally twisted endopod. Second maxilliped (Fig. 5E, F) with basis-ischium fusion incomplete. Meri of third maxillipeds each with dorsodistal spine, ventral margins unarmed.

Right cheliped (Fig. 6A, C) considerably stronger than left, but not appreciably longer; with weak hiatus between dactyl and fixed finger. Dactyl with double row of corneous-tipped spines on dorsal surface laterad of midline, at least proximally and double row of tufts of stiff setae; dorsomesial margin with row of small corneous-tipped spines, becoming more prominent distally. Palm with row of strong corneous-tipped spines on dorsomesial margin, convex dorsal surface with 6 rows of conical corneous-tipped spines; dorsolateral margin not distinctly delimited proximally, but with irregular row of corneous-tipped spines becoming marginal and extending nearly to tip of fixed finger; lateral face of palm with few spines or tubercles dorsally; mesial face with transverse rows of tubercles. Carpus with irregular row of strong corneous-tipped spines on dorsomesial margin, dorsal surface with irregular rows of corneous-tipped spines accompanied by sparse tufts of stiff setae; dorsolateral margin not distinctly delimited, but with row of corneous-tipped spines; lateral face primarily with tufts of stiff setae. Merus with 2–4 strong and 1 or 2 smaller spines on dorsodistal margin, dorsal margin with short transverse ridges and quite short stiff setae, distal-most ridge spinose; ventromesial margin with row of small spines distally replaced by short transverse row of tuberculate spines proximally; ventrolateral margin with row of corneous-tipped spines distally replaced by low protuberances proximally; ventral surface with 2 transverse rows of conical spines, largest proximally.

Left cheliped (Fig. 6B, D) with two irregular rows of corneous-tipped spines on dorsal surface of dactyl proximally becoming single row distally, dorsomesial margin and mesial face with irregular rows of tuberculate corneous-tipped spines, more numerous in proximal half. Palm with irregular row of strong corneous-tipped spines on dorsomesial margin, dorsal surface generally somewhat flattened, with 4 irregular rows of tuberculate corneous-tipped spines decreasing to 2 rows on fixed finger; dorsolateral margin not clearly delimited but with double row of tuberculate or corneous-tipped spines. Carpus with 1 prominent spine on dorsodistal margin; dorsomesial margin with strong corneous-tipped spines and tufts of stiff setae, dorsal surface with adjacent and median rows of corneous-tipped spines, interspersed with few smaller spines; dorsal surface laterad of midline with irregular rows of corneous-tipped spines extending onto lateral face dorsally. Merus with 1–3 large and 1 or 2 smaller spines on dorsodistal margin, dorsal margin with transverse ridges and setae, distal-most spinose; ventromesial margin usually with short row of corneous-tipped spines in distal half, becoming low tubercles proximally and extending onto ventral surface; ventrolateral margin with row of prominent spines in distal half, shifting onto ventral surface proximally, 1 larger tuberculate spine at proximal angle.

Ambulatory legs overreaching chelipeds by approximately half length of dactyls. Dactyls of left and right (Fig. 7A, second) similar; moderately long and stout, 1.65–2.0 length of propodi; in dorsal view slightly twisted; in lateral view slightly curved; dorsal surfaces somewhat flattened, each with double row of corneous-tipped spines and row of stiff setae, inner-most row becoming simple corneous spines distally; lateral and mesial surfaces each with longitudinal sulcus, strongest on second; lateral faces each also with row of tufts of stiff setae, and arc of 4 or 5 stiff setae proximally, mesial faces each also with row of stiff setae proximally and arc of stiff setae distally; ventral margins each with row of 4 or 5 prominent corneous spines distally, becoming very small widely-spaced spinules in proximal 0.75. Propodi each with 2–4 rows of strong corneous-tipped spines accompanied by tufts of stiff setae extending onto lateral face dorsally; mesial faces each with 1 or 2 blunt or subacute spines dorsally and tufts of stiff setae; ventrodistal margin with row of small corneous spinules or short stiff bristles. Carpi each with row of strong corneous-tipped spines on dorsal surface; lateral faces spinulose (second) or with low protuberances and tufts of stiff setae (third). Meri all with transverse rows of short stiff setae dorsally, ventral margins of second pereopods each with 1 or 2 spines; ventral margins of third unarmed. Sternite of third pereopods with row of setae on roundly subrectangular to subquadrate anterior lobe.

Telson (Figs. 11A, B) with asymmetrical posterior lobes separated by slender median cleft; terminal margins often considerably produced laterally, each with row of small calcareous spines on inner half, calcified but unarmed on outer half.

Color.—Beautiful violet (Boschi et al. 1992).

Distribution.—Chile, Strait of Magellan, Argentina, Uruguay; littoral to 150 m.

Remarks.—The holotype of *Pagurus gaudichaudii* has the abdomen and all appendages disarticulated; the fourth and fifth pereopods, including their coxae, are missing. The specimen is determined to be a male since no gonopores are present on the coxae of the third pereopods. The bottle contains two labels, an old printed one reading "*Pagurus Gaudichaudii* Edw., M. Gaudichaud, Valparaiso," and a second hand written by Bouvier indicating the reference to Milne Edwards' publication and the mention of "type." The holotype of *Pagurus barbiger*, as noted by Forest & de Saint Laurent (1968) is a young female. Its label indicates "*Eupagurus* (*Bernhardus*) *barbiger* M. Edw. et Mocquet, 1891, Mission du Cap Horn, baie Orange, 22m." The bottle, MNHN Pg 2401, also contains a second smaller female (sl = 5 mm), which is not mentioned in the original publication, and therefore cannot be considered a type specimen.

Benedict (1901) noted that A. Milne Edwards' (1891) description of *Pagurus barbiger* had come to his attention only after his own description of *Pagurus patagoniensis* (as *Eupagurus*) had been published (Benedict 1892). Based on A. Milne Edwards (1891) description and figures, Benedict (1901) pointed out several differences between *P. barbiger* and *P. patagoniensis*, but acknowledged that these differences might well be related to size and that the two might prove to be conspecific. Lagerberg (1905) formally placed *P. patagoniensis* in synonymy. Haig (1955) recognized the similarities between *P. barbiger* as described by Lagerberg (1905) and *P. gaudichaudii* (as *P. gaudichaudi*) from Chile. At Haig's request, J. Forest examined the types of both species and confirmed her suspicions. *Pagurus barbiger*, together with *P. patagoniensis* were then placed in synonymy with *P. gaudichaudii*; however, neither Lagerberg (1905) nor Haig (1955) actually examined Benedict's (1892) *P. patagoniensis*. We have now compared Benedict's syntypes with the holotypes of *P. gaudichaudii* and *P. barbiger*, as well as with specimens of *P. gaudichaudii* from *Calypso* station 170 off Rio de la Plata, and can reaffirm the conspecificity of the three taxa.

Forest & de Saint Laurent (1968) discussed the size-related variations observed in small specimens of *P. gaudichaudii*. These include longer ocular peduncles, narrower ocular acicles, shorter antennular and antennal peduncles, and stouter ambulatory legs. *Propagurus gaudichaudii* differs from the other species of the genus in several morphological attributes: the dorsal surface of the chela of the left cheliped is flattened, lacking the elevated median row(s) of spines of the other species; the carpus of the left cheliped is appreciably broader and, while armed with numerous spines, these do not form the two distinctive longitudinal rows seen in the other species; the ambulatory dactyls have only a few strong corneous spines distally, followed by widely-spaced very tiny spinules, whereas the dactyls of all three other species are each armed with a complete row of strong spines; the dorsal surfaces of the propodi of the ambulatory legs are generally flattened and each is armed with a double row of spines. In these characters, *P. gaudichaudii* approaches species of the *bernhardus* group of *Pagurus* (cf. McLaughlin 1974), which is undoubtedly why Benedict (1901) aligned *P. patagoniensis* with species like *Pagurus bernhardus* (Linnaeus 1758).

In addition to the differentiating characters of the gills, the short ocular peduncles, spinose laterodistal projections of the second segment of the antennal peduncle, and spatulate pleopodal endopods clearly unite *Propagurus gaudichaudii* with the other species assigned to the genus. The distinctive subquadrate shield and general shape of the posterior telsonal lobes of *P. gaudichaudii* appear to indicate a closer relationship to *P. deprofundis* than to either *P. haigae* or *P. yokoyai*. Although the shield is more angular in *P. gaudichaudii* than in *P. deprofundis*, both are somewhat dissimilar to the more rounded shields of *P. haigae* and *P. yokoyai*. In both *P. gaudichaudii* and *P. deprofundis* there is a tendency for the terminal margins of the telson to be produced laterally; however, while in *P. gaudichaudii* the lateral half of each lobe usually consists of a pectinate, faintly denticulate, or entire plate, this portion in *P. deprofundis*, like the median portions in both species, is often provided with spines. In *P. gaudichaudii*, the mesial faces of the palms of the chelipeds are armed with transverse rows of tubercles, not identical with, but similar to the rows of tubercles or small spines seen on the lateral surfaces of the palms of *P. deprofundis*. No comparable armature is seen on either surface of the palms of *P. haigae* or *P. yokoyai*.

Propagurus deprofundis (Stebbing 1924), new combination
Figs. 2D, E, 4B, 7B, 8A–D, 9, 11C, D

Eupagurus deprofundis Stebbing, 1924: 243, pl. 70.—Barnard, 1950: 164.—Forest, 1955: 107.
Pagurus deprofundis.—Gordan, 1956:329 (lit).
Pagurus deprofundus.—Kensley, 1981:33 (list) (misspelling).
Propagurus deprofundis.—McLaughlin & Forest, 1998, figs. 7A–K.

Holotype.—♀ (sl = 9.3 mm); 13 miles

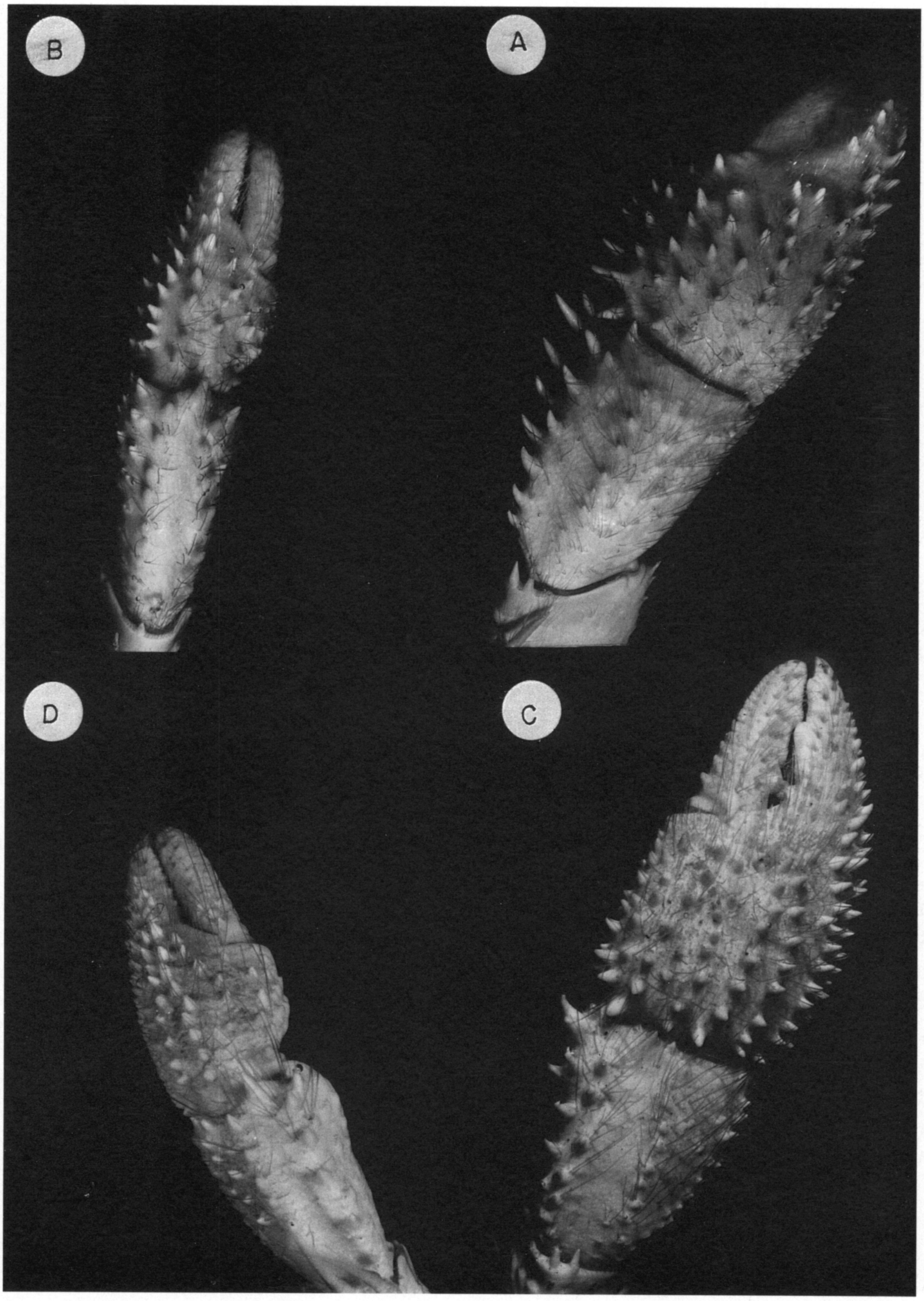

Fig. 8. *Propagurus deprofundis* (Stebbing, 1924) new combination. A, C, chela and carpus of right cheliped; B, D, chela and carpus of left cheliped. A, B, ♂ (sl = 11.2 mm), NZOI; C, D, holotype ♀ (sl = 9.3 mm), NHM 1928.12.1.245. Magnifications equal 2.8× (A), 3.0× (B), 3.8× (C), and 3.1× (D).

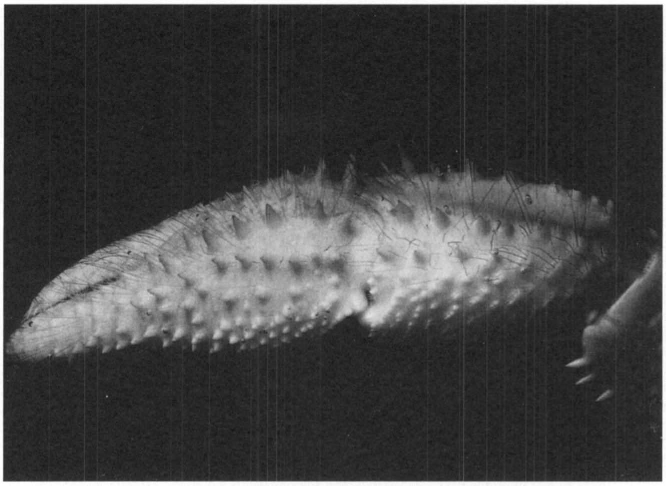

Fig. 9. *Propagurus deprofundis* (Stebbing, 1924) new combination, ♂ (sl = 11.2 mm), NZOI. Chela and carpus of left cheliped (lateral view). Magnification equal 3.0×.

northwest of Cape Morgan, South Africa, 32°42.6′S, 28°21.8′E, 457–585 m, NHM 1928.12.1.245.

Other material examined.—Philippine Islands. MUSORSTOM Philippine Expeditions: 1 ♂, 1 ♀ (sl = 9.3, 9.5 mm) sta. 44, 13°46.9′N, 120°29.5′E, 610–592 m, 24 Mar 1976, MNHN Pg 5545.—1 ♂ (sl = 7.6 mm), sta. 77, 13°48.8′N, 120°30.1′E, 552–529 m, 1 Dec 1980, MNHN Pg 5546.—1 ♂ (sl = 11.5 mm), sta. 106, 13°47′N, 120°30′E, 640–668 m, 2 Jun 1985, MNHN Pg 5547.

Indonesia. Corindon: 1 ♂, 1 ♀ (sl = 10.5, 11.5 mm), *Corindon II* Makassar Strait sta. 276, 1°54.6′S, 119°13,8′E, 456–395 m, 8 Nov 1980, MNHN Pg 5548.

Australia. Th. Mortensen's Pacific Expedition: 1 ovig. ♀ (sl = 10.2 mm), 38°05′S, 150°00′E, 366–475 m, 12 Nov 1914, ZMUC.—1 ovig. ♀ (sl = 5.8 mm), 39°10′S, 149°55′E, 366–457 m, 15 Nov 1914, ZMUC.—Museum of Victoria: 1 ♀, 3 ovig. ♀ (sl = 6.8–10.8 mm), sta. FR5/86, 38°14.9′S, 149°26.1′E, 800 m, 23 Jul 1986, J 21015.—1 ♂, 3 ovig. ♀ (sl = 5.9–8.9 mm), sta. Slope 40, 38°17.7′S, 149°11.3′E, 400 m, 24 Jul 1986, J 40397.—1 ♀ (sl = 5.9 mm), sta. Slope 46, 42°00.2′S, 148°37.7′E, 720 m, 27 Jul 1986, J 17422.—2 ♂, 1 ♀ (sl = 3.6–5.2 mm), sta. Slope 49, 41°56.5′S, 148°37.9′E, 200 m, 27 Jul 1986, J 17431.—1 ♂, 1 ♀ (sl = 5.2, 8.0 mm), sta. Slope 67, 34°43.6′S, 151°13.2′E, 450 m, 22 Oct 1988, J 40390.—3 ♀, 1 ovig. ♀ (sl = 6.2–7.4 mm), sta. Slope 84, 41°53.5′S, 148°39.1′E, 732 m, 30 Oct 1988, J 40389.—1 ♂, 2 ♀ (sl = 6.9–13.7 mm), 33°46′S, 151°49′E, 414 m, 9 Sep 1981, J 40386.—1 ♂ (sl = 12.7 mm), sta. So5/84-27, 37°59.4′S, 150°05.4′E, 452 m, 14 Oct 1984, J 40385.—2 ♂ (sl = 13.3, 10.4 mm), sta. So6/84-13, 37°45.2′S, 150°13.4′E, 426 m, 28 Nov 1984, J 21012, J 40388.—1 ♂ (sl = 11.0 mm), sta. So6/84-18, 39°17.1′S, 148°44.4′E, 580 m, 30 Nov 1984, J 40387.—1 ♂, 2 ♀ (sl = 7.3–17.1 mm), sta. So1/85-45, 37°41.5′S, 150°14′E, 458 m, 4 Feb 1985, J 40391.

New Zealand. NMNZ: 1 ♀, 2 ovig. ♀ (sl = 12.0–14.0 mm), sta. CM 149, 46°30′S, 165°14.4′E, 545–573 m, 10 Sep 1987, NMNZ Cr 8066.—1 ♂ (sl = 14.5 mm), sta. JO6/008/81, 39°29.8′S, 178°10.8′E, 529–568, 15 Apr 1981, NMNZ Cr 8097.—1 ♂ (sl = 17.0 mm), sta. SM 2/50, 42°50.5′S, 177°42.5′E, 540–499 m, 9 Nov 1975, NMNZ Cr 8099.—1 ♂, 1 ♀ (sl = 15.2, 10.9 mm), sta. BS844, 37°10.9′S, 176°38.7′E, 685–705 m, 23 Jan 1981, NMNZ Cr 7592, Cr 8211.—Northern Prawn Survey: 1 ♀ (sl = 9.7 mm), haul 14, 8 mi E White I., 640–548 m, 10 Sep 1962.—NZOI: 1 ♂ (sl = 12.4 mm), sta. C619, 43°52′S, 174°48′E, 802 m, 2 May 1961.—1 ♂ (sl = 14.7 mm), sta. D233, 38°50′S, 169°20′E, 530 m, 29 Sep 1964.—1 ♂ (sl = 12.9 mm), sta. E711, 39°18.8′S, 178°13.8′E, 490–428 m, 23 Mar 1967.—5 ♂, 1 ovig ♀ (sl = 9.0–11.8 mm), sta. E719, 38°46′S, 178°48′E, 913–750 m, 23 Mar 1967.—1 ♀ (sl = 11.8 mm), sta. E747, 40°43.2′S, 176°48.4′E, 554–569 m, 29 Mar 1967.—1 ♂ (sl = 9.9 mm), sta. E797, 45°20′S, 166°44.7′E, 471 m, 20 Oct 1967.—1 ♀ (sl = 7.8 mm), sta. E822, 46°50.6′S, 165°36′E, 682–786 m, 23 Oct 1967.—1 ♂, 1 ♀ (sl = 14.4, 12.6 mm) sta. E827, 46°35.5′S, 166°44.5′E, 532 m.—1 ovig ♀ (sl = 11.8 mm) sta. E831, 47°50.6′S, 167°03.8′E, 479 m, 25 Oct 1967.—1 ♀ (sl = 10.0 mm), sta. E876, 37°32.5°S, 177°34′E, 529–492 m, 10 Mar 1968.—1 ♀ (sl = 7.6 mm), sta. E 879, 35°19′S, 172°25′E, 762–780 m, 22 Mar 1968.—1 ♂ (sl = 10.5 mm), sta. J711, 37°59.4′S, 176°03′E, 366–472 m, 11 Sep 1974.

Hawaiian Islands. U.S. Fish Commission: 1 ♀ (sl = 7.1 mm), *Albatross* sta. 4132, 22°01.5′N, 159°21.2′W, 470–570 m, 1 Aug 1902, USNM 284748.

Diagnosis.—Shield (Fig. 4B) varying from slightly longer than broad to distinctly broader than long. Rostrum commonly triangular, usually produced beyond level of lateral projections, occasionally even developing slight, short rostral keel; usually with prominent terminal spine. Lateral projections obtusely triangular, each with strong submarginal spine. Ocular peduncles slightly less to slightly more than half shield length; moderately stout, broader at base of corneas than proximally, dorsal or dorsomesial surface usually with short transverse rows of sparse tufts of setae; corneas slightly dilated. Ocular acicles ovately or acutely triangular, dorsal surfaces somewhat concave, each with strong submarginal spine. Fully extended antennular peduncles overreach distal margins of corneas by 0.20 length of ultimate segments to 0.25 length of penultimate segments; basal segment with very strong spine on lateral surface in distal half. Antennal peduncles overreach distal margins of corneas by 0.10–0.75 length of ultimate segments, and reach approximately to distal 0.35–0.85 of ultimate segments of antennular peduncles; second segment with laterodistal projection reaching at least to distal half of fourth peduncular segment, with simple or bifid terminal spine, mesial margin with 5–9 small spines, lateral margin with tufts of long setae, dorsomesial distal angle with very strong spine; first segment with prominent spine on distolateral margin dorsally; ventrolateral margin with 1–3 spines. Antennal acicle reaching at least to mid-length of ultimate peduncular segment, usually considerably beyond, with strong terminal spine and numerous tufts of long stiff setae on mesial face. External endopodal lobe of maxillule (Fig. 2D, E) well developed, sometimes arched, but never strongly recurved. Meri and carpi of third maxillipeds each with dorsodistal spine; meri also usually with 1, occasionally with 2 spines on ventral margin, rarely unarmed.

Right cheliped (Fig. 8A, C) considerably stronger than left, but not always appreciably longer; sometimes with hiatus between dactyl and fixed finger. Dactyl with convex dorsal surface marked by transverse rows of tufts of stiff setae and often few spines proximally; dorsomesial margin with single or double row of small spines. Palm varying from moderately slender to moderately broad, with irregular double row of spines on dorsomesial margin, convex dorsal surface sparsely covered with short setae, with 6 somewhat irregular rows of spines, usually accompanied by long stiff setae; dorsolateral margin not distinctly delimited proximally, but with irregular row of spines becoming marginal and extending nearly to tip of fixed finger; lateral face of palm with distinct rows of closely-spaced tubercles or tuberculate spines particularly in ventral half. Carpus with irregular row of strong spines on dorsomesial margin accompanied by adjacent slightly irregular row of spines on dorsal surface, separated by broad nearly naked longitudinal strip from median row of shorter spines, few scattered spines laterally; dorsolateral margin rounded but with row of small spines usually becoming double row distally; lateral face sometimes with forwardly directed spines and spinules or tubercles, occasionally just low protuberances and long setae; ventral surface often with row of spines mesially and laterally. Merus with 0–3 spines on dorsodistal margin, dorsal margin with short transverse ridges; mesial face with scattered protuberances proximally; ventromesial margin usually with row of spines or tubercles, strongest proximally; lateral face with transverse sometimes spinulose ridges at least in ventral half, ventrolateral margin with row of acute or subacute spines; ventral surface often with few small and occasionally 2 large spines.

Left cheliped (Fig. 8B, D) frequently with hiatus between dactyl and fixed finger; with numerous tufts of long setae and also often with few spinules proximally on rounded dorsal surface of dactyl. Palm usually moderately slender, with median single or double row of spines on convex dorsal surface, becoming less regular on proximal half of fixed finger; dorsomesial face usually with central row of spines and nearly double row of slightly smaller spines; dorsolateral face (Fig. 9) with several irregular rows of small closely-spaced tubercles, spines or spinules, appreciably stronger dorsally, but not extending to tip of fixed finger. Carpus with 1 sometimes quite strong spine on dorsodistal margin, and occasionally with second spine directly beneath; dorsomesial margin with irregular row of moderate to strong spines and tufts of long setae, dorsal surface unarmed, slightly depressed; rounded dorsolateral margin with row of spines; lateral surface with semi-perpendicular rows of small tuberculate spines decreasing in size proximally, ventrolateral margin with row of small subacute spines. Merus with 1–3 spines at dorsodistal margin, dorsal margin and mesial face each with transverse ridges and setae, sometimes becoming multispinose ventrally on mesial face; ventromesial margin with row of spines proximally and frequently also small spine distally; lateral face with short transverse ridges becoming flattened multifid tubercles ventrally, ventrolateral margin with row of spines sometimes becoming double row proximally.

Ambulatory legs overreaching left cheliped by at least 0.75 length of dactyls. Dactyls and propodi of left and right (Fig. 7B of second) morphologically similar, but left with greater setation on lateral faces. Dactyls moderately long and stout, 1.10–1.85 as long as propodi; in dorsal view weakly to strongly twisted; in lateral view straight (second) or slightly curved (third); dorsal surfaces with transverse low protuberances and long stiff setae; lateral surfaces each with faint longitudinal sulcus and row(s) of long or moderately long setae; ventral margins each with row of 8–21 strong corneous spines. Propodi each with transverse low ridges and long stiff setae on dorsal and lateral surfaces; mesial faces of second pereopods (Fig. 7B right) each with longitudinal keel in ventral third, extending from near distal margin to mid-length, or more frequently, proximal third. Carpus of second right with row 5–8, second left with row of 3–7 spines and transverse setose ridges on dorsal surfaces; dorsal surfaces of third each with 0–5 smaller spines and transverse setose ridges in additional to strong dorsodistal spine; lateral faces all with short transverse ridges and long setae. Meri all with transverse setose ridges dorsally, ventral margins of second each with ventromesial row of spines, more numerous and stronger on left, ventrolateral distal angles each sometimes with spine; ventral margins of third unarmed or rarely with tiny spinule on ventrolateral margin and stronger spinule on ventromesial margin distally. Sternite of third pereopods with submarginal row of setae on subsemicircular to roundly subrectangular anterior lobe.

Mature females usually with dense setae on coxae of fifth pereopods. Telson (Fig. 11C, D) with asymmetrical posterior lobes separated by slender median cleft; terminal margins often considerably produced laterally, each with row of small calcareous spines becoming stronger toward outer angles, largest spines, particularly on left, somewhat hooked.

Color (in preservative).—Shield mottled white and orange. Ocular peduncles orange; ocular acicles orange basally, white distally. Antennular peduncles whitish with flagella orange. Antennal peduncles faintly orange, darkest on proximal segments. Chelipeds with orange tint, darkest on dactyls. Ambulatory legs each with orange band proximally and distally on meri; carpi, propodi and dactyls all faintly orange, darkest on distal halves of dactyls.

Habitat.—Found in a variety of gastropod shells, sometimes with anemone attached.

Distribution.—Southeastern South Africa; Tasmania and southeastern Australia, Tasman Sea, west and east New Zealand to Chatham Rise; Philippine Islands; Hawaii; 200 to 750–913 m. Bathymetric range over entire geographic range is between 450 and 750 m, with only the capture of young specimens at shallower depths.

Remarks.—As previously indicated, the only published record of rudimentary pleurobranchs on the fifth and sixth thoracic somites is that of Forest & de Saint Laurent (1968) for "*Pagurus*" *gaudichaudii*, a species superficially resembling *bernhardus* group species. Had it not been for the astute observation by Jacques Forest, Muséum national d'Histoire naturelle, (McLaughlin & Forest 1998) of the similarities between *P. gaudichaudii* and *P. deprofundis*, and the recognition in earlier (but as yet unpublished) studies of one of the present authors (MST) of similar characters in certain unidentified Indo-Pacific pagurids, this suite of species could not have been unified in a distinct genus. Following the redescription of the holotype of *P. deprofundis* (McLaughlin & Forest 1998), this enigmatic species is now recognized as having an extremely broad distribution.

The three smallest specimens examined came from the shallowest recorded depth, 200 m off Tasmania. Of these, the tiniest was a male (sl = 3.5 mm) with the gonopores barely visible, suggesting immaturity; however, another male that was only slightly larger (sl = 3.6 mm) had well marked gonopores. Pleopod development in these two males was comparable. Females were ovigerous at shield lengths as short as 5.8 and 5.9 mm.

Not only has marked variation been observed among 25 males, 22 non-ovigerous and 13 ovigerous females, as is indicated in the diagnosis, but a few abnormalities have been also noted. One specimen (sl = 10.0 mm) from the vicinity of the Solander Trough, southwestern New Zealand, has well developed female gonopores and pleopods, but also one male gonopore. Another female from the Solander Trough has a normal left cheliped, but a right that is nearly identical to it. One male specimen (sl = 14.5 mm), collected of Napier on the east side of the North Island of New Zealand has four left pleopods, that of the second somite with subequal rami as seen in females; however, no external evidence of a rhizocephalan infestation could be detected that might have had a feminizing effect. Another male (sl = 11.0 mm), collected in the same general vicinity, has a weakly produced, obtusely triangular, terminally rounded rostral lobe, that is in marked contrast to the prominent, triangular, acute rostrum seen in other specimens. The female specimen from the Makassar Strait, Indonesia, has much shorter ocular peduncles and antennal acicles than does the male from the same station. A similar condition has been observed in one of the Philippine specimens; however in this specimen, the

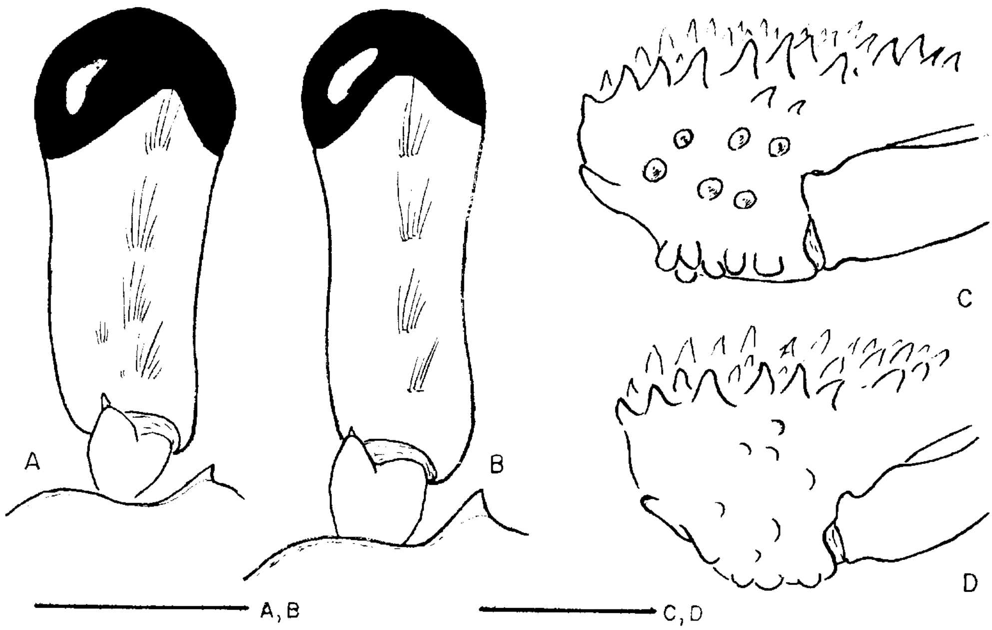

Fig. 10. A, C, *Propagurus haigae* (McLaughlin, 1997) new combination, A, ♂ (sl = 10.1 mm), MNHN-Pg 5311; C, ♀ (sl = 12.1 mm), MNHN-Pg 5310 (bis). B, D, *Propagurus yokoyai* (Makarov, 1938) new combination: B, ♂ (sl = 10.8 mm), MNHN-Pg 2277; D, ♂ (sl = 12.0 mm), MNHN-Pg 3651. A, B, right ocular peduncle portion of anterior margin of shield and right lateral projection; C, D, dorsomesial view of palm of left cheliped. Scales equal 3 mm (A, B) and 5 mm (C, D).

shortened ocular peduncle and antennal acicle are present only on one side of the animal. We do not believe that these latter two specimens represent extremes in variation, but rather abnormalities.

Propagurus haigae (McLaughlin 1997), new combination

Figs. 4C, 7C, 10A, C, 11E, F, 12A, B

Pagurus haigae McLaughlin, 1997:533, figs 27a–h, 43a–d.

Holotype.—♂ (sl = 18.6 mm), KARUBAR sta. CP 16, 05°17′S 132°50′E, 315–349 m, 24 Oct 1991, MNHN Pg 5310.

Paratypes.—1 ♀ (sl = 12.1 mm), KARUBAR sta. CP 16, 05°17′S 132°50′E, 315–349 m, 24 Oct 1991, MNHN Pg 5310.— 1 ♂ (sl = 10.1 mm with branchial bopyrid), sta. CP 26, 05°34′S, 132°52′E, 265–302 m, 26 Oct 1991, MNHN Pg 5311.— 1 ♂ (sl = 7.3 mm), sta. CP 26, 05°34′S, 132°52′E, 265–302 m, 26 Oct 1991, SNHM 4812.—1 ♂ (sl = 11.5 mm), Sta CC 41, 07°45′S, 132°42′E, 401–393 m, 28 Oct 1991, USNM 276014.

Other material examined.—New Caledonia: 2 ♂ (sl = 5.1, 6.3 mm, 1 with branchial bopyrid), SMIB 4, sta. DW 58, 22°59.8′S, 167°24.2′E, 560 m, 9 Mar 1989, MNHN Pg 5549.

Indonesia. Danske Kei Expedition: 1 ♂ (sl = 18.7 mm), 05°28′S, 132°36′E, 385 m, 12 May 1922, ZMUC.—U.S. Fish Commission: 1 ♀ (sl = 11.2 mm), *Albatross* sta. 5623, 7.5 mi. NE of S Makyan Is., 00°16.5′N, 127°30′E, 497 m, 29 Nov 1909, USNM 284749.

Australia. 1 ♂ (sl = 17.1 mm), *Soela* sta. 0685-27, 20°24′S, 152°57.8′E, 511–508 m, 22 Nov 1985, NTM Cr 6864.—Th. Mortensen's Pacific Expedition: 1 ♂ (sl = 15.7 mm), 37°45′S, 150°10′E, 274–475 m, 14 Sep 1914, ZMUC.—1 ♂ (sl = 4.8 mm), 38°05′S, 150°00′E, 347–439 m, 12 Sep 1914, ZMUC.—1 ♂ (sl = 12.9 mm),

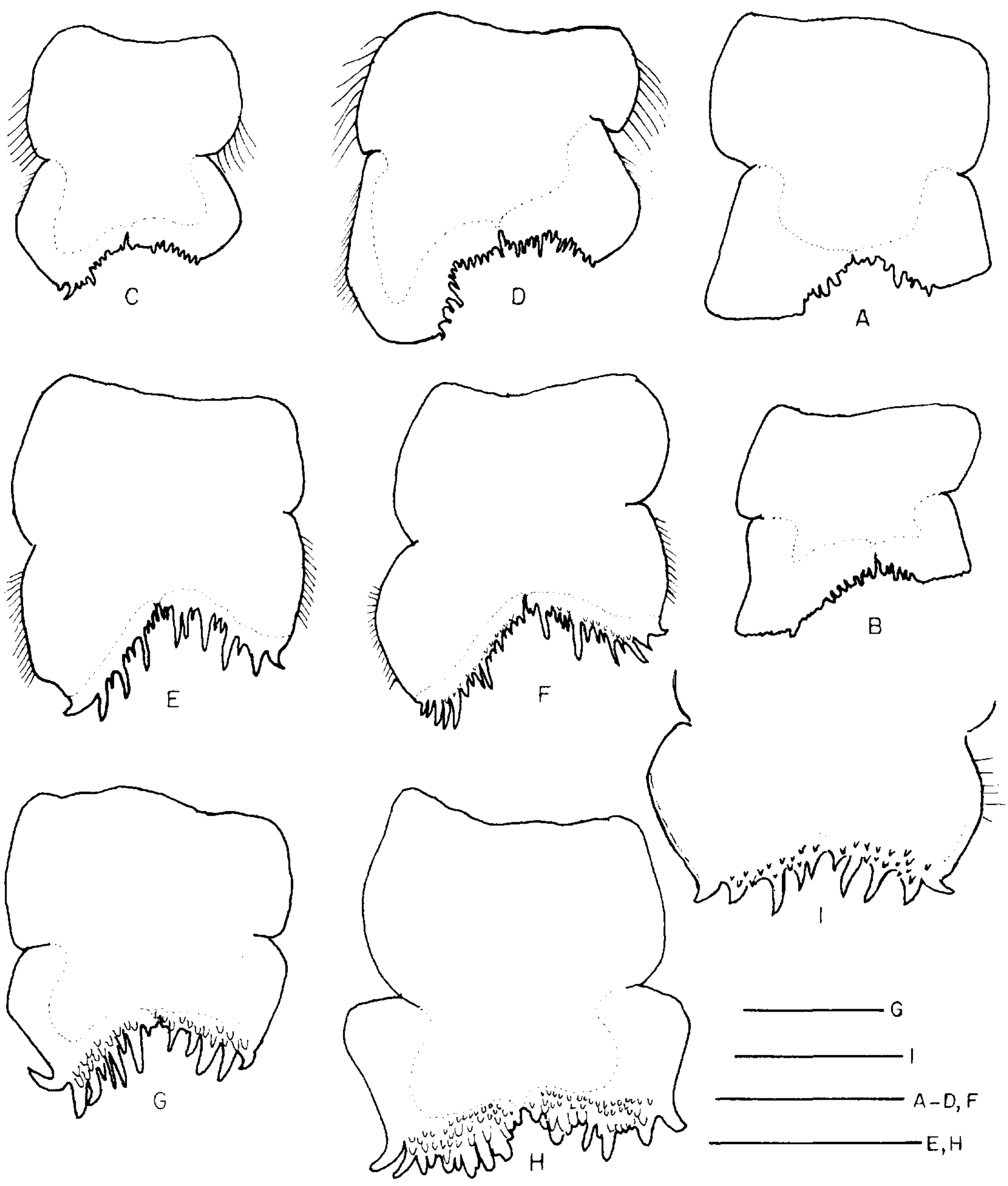

Fig. 11. Telsons. A, B, *Propagurus gaudichaudii* (H. Milne Edwards, 1836) new combination. A, ♀ (sl = 16.0 mm), MNHN-Pg 2852, B, syntype of *Pagurus patagoniensis* (Benedict, 1892), ♀ (sl = 11.8 mm), USNM 16772; C, D, *Propagurus deprofundis* (Stebbing, 1924) new combination, A, ♂ (sl = 11.2 mm), NZOI; D, holotype ♀ (sl = 9.3 mm), NHM 1928.12.1.245; E, F, *Propagurus haigae* (McLaughlin, 1997) new combination, ♂ (sl = 17.1 mm), NTM Cr 6864, F, paratype ♂ (sl = 11.5 mm), USNM 276014; G–I, *Propagurus yokoyai* (Makarov, 1938) new combination, G, ♂ (sl = 11.5 mm), OMNH Ar 1941, H, ovig. ♀ (sl = 9.6 mm), CBM-ZC 3390, I, juvenile ? ♂ (sl = 5.0 mm), MNHN-Pg 2198. Scales equal 1 mm (I), 2 mm (E, H) and 5 mm (A–D, F, G).