



Fig. 12. Carpi and chelae of chelipeds. A, B, *Propagurus haigae* (McLaughlin, 1997) new combination, ♂ (sl = 17.1 mm), NTM Cr 6864, A, right, B, left. C, D, *Propagurus yokoyai* (Makarov, 1938) new combination, ♂ (sl = 11.5 mm), OMNH Ar 1941, C, right, D, left. Magnifications equal 1.6× (A, B), and 2.5× (C, D).

38°10'S, 149°55'E, 366–475 m, 11 Sep 1914, ZMUC.—Museum of Victoria: 1 ♂ (sl = 9.6 mm), 38°00'S, 141°00'E, 540 m, Jan 1981, J 40407.—1 ♂ (sl = 5.7 mm), sta. Slope 40, 38°17.7'S, 149°11.3'E, 400

m, 24 Jul 1986, J 40397.—1 ♂ (sl = 10.6 mm), sta. So5/84-27, 37°59.4'S, 150°05.4'E, 452 m, 14 Oct 1984, J 40402.—1 ♀ (sl = 18.7 mm), sta. So5/84-51, 41°03'S, 144°20'E, 520–480 m, 20 Oct 1984, J

21071.—1 ♂, 1 ovig. ♀ (sl = 11.7, 14.1 mm), sta. So6/84-18, 39°17.1'S, 148°44.4'E, 580 m, 14 Sep 1984, J, 40393, J 40404.

Diagnosis.—Shield (Fig. 4C) with length equaling width or longer than broad. Rostrum usually broadly triangular, terminally rounded or acute, with or without terminal spinule. Lateral projections triangular, with strong marginal or submarginal spine. Ocular peduncles (Fig. 10A) 0.50–0.75 length of shield, slightly broader distally; corneas weakly dilated; dorsal surfaces frequently with row of sparse setae. Ocular acicles roundly triangular, terminating subacutely and with strong submarginal spine. Distal margins of corneas usually not reaching to mid-length of fully extended ultimate segment of antennular peduncle. Antennal peduncles overreaching distal margins of corneas by 0.10–0.50 length of ultimate segments; second segment with laterodistal projection reaching to or beyond mid-length of fourth peduncular segment, terminating in simple or bifid spine and usually with 3–6 spines on mesial margin sometimes partially obscured by thick setae; dorsomesial distal angle with acute spine; first segment with spine on lateral margin distally, ventrolateral margin with 3–6 small spines laterally and distally. Antennal acicles reaching distal half of ultimate peduncular segments, and usually considerably beyond distal margin of corneas; terminating in acute spine, mesial margin with row of tufts of stiff setae. Maxillule with external lobe of endopod varying from vestigial to well developed. Meri, and usually also carpi, of third maxillipeds each with small dorsodistal spine.

Chelipeds grossly unequal; spines of chelae and carpi often practically obscured by tufts of long dense setae. Right cheliped (Fig. 12A) with dactyl slightly overlapped by fixed finger; dorsal surface convex, with median row of small spines decreasing in size distally but usually extending nearly to tip; dorsomesial margin with row of moderate to small spines also decreasing in size

distally. Palm with dorsomesial margin usually only weakly delimited by quasi-double row of moderate to strong spines, frequently 1 more prominent spine or tubercle at dorsoproximal angle, convex dorsal surface with 8 or 9 irregular rows of moderate to strong spines; dorsolateral margin not distinctly delimited except on fixed finger; dorsal surface of fixed finger with median row of spines decreasing in size distally, mesial face of palm and lateral and ventral surfaces of palm and fixed finger usually all with spines or low, sometimes spinulose protuberances and tufts of long setae, occasionally unarmed. Carpus moderately broad and short (distal margin:dorsomesial margin = 2:3–3:4); with row of usually strong spines on dorsomesial margin, dorsal surface with few to numerous small spines or low sometimes spinulose protuberances and tufts of long setae, distal margin with row of spinules and few slightly larger spines; dorsolateral margin not delimited, lateral face with low sometimes spinulose protuberances and tufts of long setae, laterodistal margin with row of small spines; mesial face with few spines dorsally, scattered low protuberances and setae ventrally, mesiodistal margin sometimes with row of very small blunt spines. Merus with 2–4 spines on dorsodistal margin, dorsal surface with few short transverse rows of setae; ventrolateral margin with row of small spines not extending to proximal margin but frequently terminating proximally in 1 or 2 larger blunt spines or tubercles; ventromesial margin with few small spines, sometimes 1 or 2 larger tubercles at proximal angle.

Left cheliped (Fig. 12B) with ventral surfaces of palm, fixed finger and dactyl all with tufts of long setae; dorsomesial margin of dactyl not delimited or with 2 or 3 small spines proximally, dorsal midline unarmed or with few spinules or spinulose tubercles in proximal half. Palm triangular in cross-section, dorsal surface with row of strong spines decreasing in size distally and usually extending to distal half, occasionally

nearly to tip, of fixed finger; dorsolateral margin with single or double row of strong spines, decreasing in size and becoming single row on fixed finger; dorsolateral face with numerous strong spines; dorsomesial face (Fig. 10C) usually with smaller spines or spinulose tubercles partially obscured by tufts of setae, dorsomesial margin with row of 3 or 4 spines or tubercles. Carpus with row of acute spines on dorsolateral margin, dorsodistal margin with 1 strong spine, dorsomesial margin with row of smaller spines, strongest proximally, all partially obscured by long setae; laterodistal margin with few spines dorsally, lateral face with low frequently spinulose protuberances and long setae, ventrolateral margin with row of spines and moderately dense row of long setae; ventromesial margin with 2–4 small, often blunt spines distally. Merus with short transverse rows of long setae on dorsal margin; ventromesial margin with few small spines; ventrolateral margin with row of very strong acute spines sometimes interspersed with shorter spines and row of long setae, frequently 1 or pair of stronger acute or blunt spines on each margin proximally.

Ambulatory legs with dactyls (Fig. 7C of right second) 1.2–1.5 as long as propodi; in dorsal view, slightly to moderately twisted; in lateral view, somewhat curved ventrally; dorsal margins each with rows of long setae, often interspersed with corneous bristles; lateral faces each with weak to prominent longitudinal sulcus and few setae (second and third right), moderately dense but randomly placed long setae on third left; mesial faces often also with faint longitudinal sulcus, second pereopods flanked dorsally and ventrally by long setae, and usually also with dorsal and/or ventral row of corneous spines, third pereopods with row of corneous spines often interspersed with tufts of setae dorsally and medially; ventromesial surfaces each with 8–17 strong corneous spines, increasing in length distally, but partially obscured by long setae. Propodi each with row of low transverse protuberances and tufts of setae dor-

sally and ventrally; lateral faces each frequently with small tubercle at proximal margin medially or dorsally, second and third right pereopods each with 2 or 3 longitudinal rows of sparse tufts of setae, left third with entire surface covered by (but not extremely dense) short transverse rows of moderately short stiff setae; ventrodistal margins each with 1 or 2 small corneous spinules. Carpi of second pereopods each with row of 4–8 spines partially obscured by long setae on dorsal surface, spines of left often smaller and fewer in number, third pereopods each with dorsodistal spine, dorsal surface unarmed or often with 1 to several much smaller spines partially obscured by row of tufts of setae; lateral faces also with 2 or 3 longitudinal rows of sparse tufts of setae. Meri each with several transverse rows of long setae dorsally and ventrally, second also with single or double row of small spines on each ventral margin. Sternite of third pereopods with few long setae on subsemicircular anterior lobe.

Telson (Fig. 11E, F) with posterior lobes somewhat asymmetrical, separated by small median cleft; terminal margins slightly to strongly oblique, each with row of 2–5 strong calcareous spines often interspersed with smaller calcareous or corneous spines, dorsal surfaces adjacent to terminal margins sometimes with row of accessory calcareous spinules, more frequent and/or abundant in larger specimens; lateral margins usually with few to numerous corneous spinules and occasionally calcareous spines.

Color (in preservative).—General overall orange tint; somewhat mottled on shield. Antennal flagella with alternating series of 8–10 transparent articles followed by similar number of burnt-orange. Meri of chelipeds and ambulatory legs with darker orange, but with white band on distal margin dorsally and laterally.

Habitat.—Variety of gastropod shells, sometimes with accompanying anemone.

Distribution.—Off Makyan, Kai, and Tamimbar Islands, Indonesia; New Caledonia;

Marion Plateau, Queensland, Australia; western Tasman Sea; 265 to 580 m.

Remarks.—The quadriserial gill structure of *P. haigae* is not readily discernible in casual observation, as evidenced by McLaughlin's (1997) initial assignment of the species to *Pagurus*. The external branches of the lamellae of the arthrobranchs of the fourth pereopods are quite short, and deliberate manipulation is necessary to make them apparent. Even more easily overlooked is the presence of rudimentary pleurobranchs on the fifth and sixth thoracic somites in what would appear to be a very typical *Pagurus*-like species. It should also be noted that in McLaughlin's figure (1997, Fig. 27) the lettering for the mesial faces of the dactyls of the second and third pereopods is reversed; fig. 27c corresponds to the legend for 27e and vice versa.

McLaughlin (1997) pointed out the marked similarities between *P. haigae* and *P. yokoyai*, but suggested that color, telson armature, strength of cheliped meral spines, number of spines on the ventral margins of the dactyls of the ambulatory legs, and length-width ratios of the carpus of the right cheliped would readily separate the two species. Now having examined a number of larger specimens of *P. haigae*, and similarly, smaller specimens of *P. yokoyai*, those distinctions are not as reliable as previously presumed. Although the carpus of the right cheliped is definitely longer and more slender in large male specimens of *P. yokoyai*, that is not the case in smaller specimens of either sex. However, in *P. haigae*, the relative proportions do not change appreciably with size, thus the character can be an aid in recognition of large males (sl \geq 11 mm). The meri of the chelipeds of *P. yokoyai*, like *P. haigae*, may have one or two prominent posterior spines on the ventral margins. While the number of spines on the ventral margins of the dactyls of the ambulatory legs usually is fewer in *P. yokoyai*, there is sufficient variation that their numbers do overlap spine numbers in smaller specimens (sl \leq 10 mm) of *P. hai-*

gae. The generally shorter and distally slightly broadened ocular peduncles (Fig. 10A), the more spinose dorsomesial face of the palm of the left cheliped (Fig. 10C), and the armature of the telson (Fig. 11E, F) afford the best identifying morphological characters; however, even these are subject to some variation. In the case of the telson, larger specimens of *P. haigae* tend to add accessory spinules, while similarly larger specimens of *P. yokoyai* lose them. Although living color is not known for *P. haigae*, the residual colors in preservative differ appreciably from the coloration reported for *P. yokoyai*, particularly the presence in the latter species of a proximal patch of color on the ocular peduncles that has not been observed in specimens of *P. haigae*.

Specimens of *P. haigae* from the Tasman Sea differed from the Indonesian specimens in usually having a less acute rostrum, and often slightly broader shields. At two stations in the Tasman Sea, Slope 40, and So6/84-18, *P. haigae* and *P. deprofundis* occurred sympatrically; however, *P. haigae* is more restricted, both geographically and bathymetrically than *P. deprofundis*.

Propagurus yokoyai (Makarov 1938),
new combination

Figs. 4D, 7D, 10B, D, 11G-I, 12C, D

Eupagurus gracilipes Yokoya, 1933:89, fig. 33; 1939:281 [not *Pagurus gracilipes* (Stimpson, 1858)].

Pagurus yokoyai Makarov, 1938:185; 1962:175.—Okada et al., 1966:138.—Miyake, 1978:140, figs. 44, 45; 1982:131, pl. 44, fig. 1.—1991:131, pl. 44, fig. 1.—Baba, 1986:209, 305, fig. 154.—McLaughlin, 1997:536, fig. 27i.

Eupagurus yokoyai.—Miyake, 1951:138.

Pagurus gracilipes (Yokoya).—Gordan, 1956:330 (lit.) [not *Pagurus gracilipes* (Stimpson, 1858)].

Material examined.—Japan. 2 ♂ (sl = 14.0, 14.8 mm), southeast of Katsuyama-Ukishima, Boso Peninsula, 140–220 m, 10 May 1995, coll. T. Komai & M. Miya,

CBM-ZC 1668.—1 ♂, 1 ovig ♀ (sl = 11.5, 8.4 mm) off Mie Pref., 100–200 m, Jan 1977, coll. S. Habu, OMNH Ar 1941, Ar 1944.—2 ♂, 1 ♀ (sl = 7.6–9.4 mm) off Mie Pref., 100–200 m, Jan 1977, coll. S. Habu, OMNH Ar 1942, Ar 1943, OMNH Ar 1945.—1 ♂ (sl = 8.5 mm), Kushimoto, Wakayama, 150 m, 23 May 1989, PMcL.—2 juveniles, 10 ♂, 1 ♀, 8 ovig. ♀ (sl = 5.0–12.0 mm), Tosa Bay, to-300 m, 1963–1966, coll. K. Sakai, MNHN Pg 2194–2200, Pg 2277, Pg 3650–3651.—1 ovig. ♀ (sl = 9.6 mm) off Kochi, Tosa Bay, Shikoku, 33°17.1'N, 133°40.2E, 150–154 m, 5 Mar 1993, coll. K. Sasaki, CBM-ZC 3390.—2 ♂, 1 ♀ (sl = 7.6–9.4 mm), off Kochi, Tosa Bay, 146–150 m, 7 Oct 1992, coll. K. Sasaki, CBM-ZC 3458.

Diagnosis.—Shield (Fig. 4D) slightly to considerably longer than broad. Rostrum broadly triangular or rounded, not produced to level of lateral projections, with or without terminal spinule frequently obscured by tuft of setae. Lateral projections triangular, very prominent, with strong marginal or submarginal spine. Ocular peduncles 0.55–0.65 length of shield, not noticeably broader distally (Fig. 10B); corneas usually not dilated; dorsal surfaces each with sparse row of setae. Ocular acicles roundly triangular, terminating subacutely and with small submarginal spine. Distal margins of corneas usually reaching to or beyond mid-length of fully extended antennular peduncles. Antennal peduncles overreaching distal margins of corneas by 0.25–0.50 length of ultimate segments; second segment with laterodistal projection reaching to or beyond distal half of peduncular fourth segment, terminating in simple or bifid spine and with 2–4 spines on mesial margin; dorsomesial distal angle with prominent spine; first segment with spine on lateral margin distally, ventrolateral margin with 1–3 very small spines laterally and distally. Antennal acicle reaching to or beyond distal half of ultimate peduncular segment, terminating in acute spine, mesial margin with row of tufts of stiff setae. Maxillule with external lobe

of endopod well developed. Meri and carpi of third maxillipeds unarmed or each with very small dorsodistal spine.

Chelipeds grossly unequal; spines of chelae and carpi usually with small corneous tips and often practically obscured by tufts of long stiff setae. Right cheliped (Fig. 12C) usually with distinct hiatus between dactyl and fixed finger; tip of dactyl slightly overlapped by fixed finger; dorsal surface convex, with median row of strong spines decreasing in size distally but extending nearly to tip; dorsomesial margin with row of strong spines also decreasing in size distally. Palm with dorsomesial margin usually only weakly delimited by quasi-double row of strong spines, frequently 1 more prominent spine or tubercle at dorsoproximal angle, convex dorsal surface with 7 or 8 irregular rows of moderate to strong spines; dorsolateral margin not distinctly delimited except on fixed finger; dorsal surface of fixed finger with several spines proximally and median row of spines decreasing in size distally, mesial face of palm and lateral and ventral surfaces of palm and fixed finger all with low sometimes spinulose protuberances and tufts of long setae, or occasionally unarmed. Carpus moderately broad and short in females and small males (2:3–3:4), but becoming elongate and slender in males (1:2–3:5) with increasing size; with row of moderate to strong spines on dorsomesial margin, dorsal surface with few to numerous smaller spines or low sometimes spinulose protuberances or bifid tubercles and tufts of long setae, distal margin with row of minute or small spinules and few slightly larger spines; dorsolateral margin not delimited, lateral face with low sometimes spinulose protuberances and tufts of long setae, laterodistal margin with blunt tubercles or prominent spines; mesial face with few spines dorsally, scattered low protuberances or spines and setae ventrally, mesiodistal margin sometimes with row of small blunt or subacute spines. Merus with 2–4 spines on dorsodistal margin, dorsal surface with few short unarmed, spinose, or spi-

nulose transverse ridges with setae; ventrolateral margin with row of small spines not extending to proximal margin, but frequently terminating proximally with 1 or 2 prominent spines; ventromesial margin with few small spines, sometimes 1 or 2 larger spines proximally.

Left cheliped (Fig. 12D) with ventral surfaces of palm, fixed finger and dactyl all with few widely-spaced tufts of long setae; dorsomesial margin of dactyl unarmed or with short row of small spines in proximal half; dorsal midline unarmed, surface with short transverse, sometimes spinulose ridges and tufts of stiff setae. Palm triangular in cross-section, dorsal surface with row of strong spines decreasing in size distally, usually extending nearly to tip of fixed finger; dorsolateral margin with irregular single or double row of strong spines, decreasing in size and becoming single row on fixed finger; dorsolateral face with 2 irregular rows of strong spines; dorsomesial face (Fig. 10D) unarmed or with low protuberances partially obscured by tufts of setae, dorsomesial margin with row of 3–5 blunt spines or tubercles. Carpus moderately long and slender; with row of acute, usually very strong spines on dorsolateral margin, dorsodistal margin with 1 strong spine, dorsomesial margin with row of smaller spines, all partially obscured by long setae; laterodistal margin with 1 to few spines dorsally, lateral face with low frequently spinulose protuberances and long setae, ventrolateral margin with few low tubercles or row of spines accompanied by long setae; ventromesial margin with 2–4 small, often blunt spines. Merus sometimes with prominent dorsodistal spine, short transverse rows of long setae on dorsal margin; ventromesial margin with few small spines, strongest proximally; ventrolateral margin with row of very strong acute spines sometimes interspersed with shorter spines accompanied by long setae, frequently 1 or 2 stronger acute or blunt spines proximally.

Ambulatory legs with dactyls (Fig. 7D of right second) 1.20–1.75 as long as propodi;

in dorsal view, moderately to strongly twisted; in lateral view, somewhat curved ventrally; dorsal margins each with transverse rows of long stiff setae; lateral faces each with weak to prominent longitudinal sulcus and few setae (second and third right), moderately dense long setae flanking sulcus on third left; mesial faces each also with faint longitudinal sulcus, flanked dorsally and also occasionally ventrally by row of corneous spines and with ventral row of setae; ventromesial surfaces each with 5–15 strong corneous spines. Propodi each with row of low transverse protuberances and tufts of setae dorsally and ventrally; second and third right pereopods each with 2 or 3 longitudinal rows of sparse tufts of setae, left third with entire surface covered (moderate density) by short transverse rows of moderately short to moderately long stiff setae. Carpi of second pereopods each with row of 5–7 spines partially obscured by long setae on dorsal surface, spines of left occasionally smaller and fewer in number; third pereopods each with dorsodistal spine, dorsal surfaces often unarmed or often 1 to several much smaller spines partially obscured by row of tufts of setae; lateral faces also with 2 or 3 longitudinal rows of sparse tufts of setae. Meri each with several transverse rows of long setae dorsally and ventrally; second also with single or double row of small spines on ventral margin. Sternite of third pereopods with few long setae on subsemicircular or subquadrate anterior lobe.

Telson (Fig. 11G–I) with posterior lobes asymmetrical, separated by small median cleft; terminal margins slightly to strongly oblique, each with row of strong calcareous spines usually interspersed with smaller calcareous spines and with additional rows of much smaller spines on adjacent surfaces; lateral margins usually with chitinous or calcareous, frequently spinose or spinulose plate.

Color.—Ocular peduncles purple with red patch proximally. Antennular and antennal peduncles light red, with scattered

red-brown spots. Antennal flagellum minutely mottled with dark and light red-brown. Shield red-brown; cervical groove and neighboring parts dark red-brown; abdomen light red-brown. Chelipeds and ambulatory legs purplish-red with proximal part of each segment and distal part of meri red (Miyake 1978).

Habitat.—Collected on clay, sand, or muddy and shell bottoms. Shells often carrying one or two anemones.

Distribution.—Sagami and Suruga Bays, Boso Peninsula, Kushimoto, southern Kii Peninsula, Tosa Bay, Bungo Strait, Japan; 38–400 m.

Remarks.—As previously noted, males of *P. yokoyai* exhibit a sexually dimorphic lengthening and narrowing of the carpus right cheliped, with a corresponding narrowing of the chela. Additionally, two of the 18 adult males examined, one from Tosa Bay and one from Kushimoto, had female-like second left pleopods developed, but neither had any external evidence of rhizocephalan infection. The males gonopores of both specimens were smaller than usually observed in normal males, but both were small individuals, with shield length of only 8.3 and 8.5 mm respectively. Neither showed any indication of female gonopores.

Although *P. deprofundis* has now been reported from both the Philippine and Hawaiian Islands, and a specimen of *P. haigae* was collected at a latitude of 00°30.5'N, *P. yokoyai* is the only species of the genus recognized to date that has been reported exclusively from the temperate northern hemisphere. As discussed above, *P. yokoyai* most closely resembles *P. haigae*, and is readily distinguished from the latter species only by color and a combination of morphological characters: the ocular peduncles are usually slightly longer and the antennular peduncles shorter in *P. yokoyai*; the spines on the dorsal surfaces of both chelae are usually larger and less numerous in this species and the mesial face of the palm of the left is commonly unarmed; in large

males (sl \geq 10.0 mm) the carpus of the right cheliped becomes distinctly longer and narrower. In small specimens of *P. yokoyai* the telson has two to four rows of small accessory spines and spinules. In larger specimens this number may decrease to only a very small, irregularly double row. In contrast, accessory spinules have been observed forming a single row in some specimens of *P. haigae*. Both species bear a superficial resemblance to the North Pacific *capillatus* group species of *Pagurus* (cf. McLaughlin 1974); however, the quadrilateral gill structure and rudimentary pleurobranchs on the fifth and sixth thoracic somites immediately set *Propagurus* species apart.

Discussion

Of the four species now assigned to *Propagurus* new genus, in only one had the gill structure and number previously been documented; all were still assigned to the genus *Pagurus*. The overall morphological similarities of these *Pagurus*-like species with numerous taxa assigned to that genus, together with the ease in which the quadrilateral gill structure and rudimentary pleurobranchs can be overlooked, makes it quite possible that *Propagurus* is far more speciose than is currently recognized.

Three of the four recognized species are regionally endemic. *Propagurus yokoyai* has been reported in eastern Japanese waters from Sagami Bay and the Boso Peninsula southward to the Bungo Straits, but over the broad bathymetric range of 38 to 400 meters. Our specimens were all collected in the middle of this geographic range, and generally also in its bathymetric range. *Propagurus haigae* has been found in a band extending from the Banda and Arafura Seas of Indonesia southeastward as far as New Caledonia, and southward along the eastern coast of Australia to Tasmania. All known specimens have been collected from depths ranging from 265 to 580 meters. The South American *P. gaudichaudii*

is reported off the west coast of Chile, from as far north as Valparaiso southward through the Strait of Magellan and northward along the eastern coast of Argentina to Uruguay. Like *P. yokoyai* this species is found at relatively shallow depths. In particularly striking contrast is the geographic distribution of *P. depfundis*, although its bathymetric range is also the greatest. Described originally from a single specimen collected off the southeastern coast of South Africa (Stebbing 1924), its range extends eastward and southward to southeastern Australia where it is quite abundant. It is equally abundant in the waters of both western and eastern New Zealand, and while not yet known from tropical western Pacific waters, it is clearly represented in Philippine waters and as far eastward as Hawaii. There are very few pagurid species known to have such a broad geographic range.

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