Reassessment of *Pagurus pilosipes* (Stimpson), Supplemental Description of *P. insulae* Asakura, and Descriptions of Three New Species of *Pagurus* from East Asian Waters (Crustacea: Decapoda: Anomura: Paguridae)

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Abstract Critical examination of samples from Japan and Taiwan, including those published by previous workers, revealed that the name Pagurus pilosipes (Stimpson, 1858) has been assigned to several small hermit crab species characterized by spinose right cheliped and striped color pattern of the ambulatory legs. Pagurus pilosipes is redescribed and illustrated on the basis of the topotypic specimens from Okinawa Island, Ryukyu Islands. A neotype is designated for P. pilosipes in the interest of nomenclatural stability, as the holotype was presumably destroyed by the Chicago fire in 1871. The type series of Pagurus insulae Asakura, 1991, which was compared with P. pilosipes in the original description, was also reexamined for comparison. It has been found that the original description by Asakura (1991) omitted important morphological variations, which make the diagnostic features proposed by him unreliable. Additionally, the original illustrations provided by Asakura are not consistent with the illustrated specimens in several important details. Therefore, a supplemental description and full illustrations are given for P. insulae. Three new species of Pagurus mistakenly identified as P. pilosipes, P. erythrogrammus, P. nigrivittatus and P. quinquelineatus, are described and illustrated. Differences among the five species are discussed. Pagurus pilosipes and P. insulae are so far restricted to Okinawa Island and to Ogasawara Islands, respectively, while the three new species are distributed in warm temperate regions in Japan (P. nigrivittatus sp. nov. is recorded also from northeastern Taiwan and Korea). All the five species occur in shallow waters including the intertidal zone, although P. erythrogrammus sp. nov. extends the bathymetric range to 75 m.

Key words: Crustacea, Decapoda, Anomura, Paguridae, Pagurus, new species, East Asian waters.

Stimpson (1858) described a number of new species of hermit crabs from the Pacific Ocean, amongst them is *Pagurus pilosipes* (as *Eupagurus*) from Loo-Choo (=Okinawa Island, Ryukyu Islands). Stimpson's original description of *P. pilosipes* (repeated in a posthumous publication in 1907) was very brief, contrasting it with *P. hirsutiusculus* (Dana, 1851) and *P. samuelis* (Stimpson, 1858). The only characters he reported, which might have been considered as diagnostic, included the spinulose dorsal surface of the chelipeds and the longitudinal red stripes on the ambulatory legs. Several workers have reported *P. pilosipes* from warm temperate waters in East Asian waters: Honshu and Kyushu mainland of Japan (Miyake, 1978, 1982; Miyake and Imafuku, 1980; Takeda, 1986; Asakura, 1995; Minemizu, 2000); East China Sea (Miyake, 1978); Korea (Oh, 1983); and China (Wang, 1994). However, no specimens referable to Stimpson's taxon have been rediscovered from the subtropical Okinawa Islands since the original description.

Recently, Asakura (1991) described a new species, *Pagurus insulae*, from Ogasawara Islands. He compared the new species with *P. filholi* (de Man, 1887) (as *P. geminus* McLaughlin, 1976) and a species believed at that

time to represent *P. pilosipes*. However, Komai and Osawa (2001) indicated that specific confusion existed among specimens referred to *P. pilosipes* by Miyake (1978) and that the identity of the true *P. pilosipes* remained unclear.

Reexamination of a part of the material from Sagami Bay, central Honshu mainland of Japan, identified with P. pilosipes by Miyake (1978), revealed that six pagurid species were confounded, including three previously described species [Pagurus proximus Komai, 2000, P. decimbranchiae Komai and Osawa, 2001, and Propagurus obtusifrons (Ortmann, 1892)], two undetermined species of Pagurus, and one unidentified species of Nematopagurus. Furthermore, it has been found that the specimens from various localities in Japanese mainland referred to P. pilosipes by Miyake and Imafuku (1980), Miyake (1982), Takeda (1986), Asakura (1991, 1995) and Minemizu (2000) can not be assigned to any of the six species contained in Miyake's (1978) material referred to P. pilosipes. As has been the case with many of Stimpson's species, the type material of P. *pilosipes* presumably had been destroyed by Chicago fire in 1871 (cf. Evans, 1967). Therefore, material from the type locality was necessary to determine the correct identity of P. pilosipes. Fortunately, four topotypic specimens, which agreed with Stimpson's (1858) original description of P. pilosipes in the armature of the chelae and color of the ambulatory legs were discovered in the collection of decapod crustaceans from the Ryukyu Islands made by the author. Comparison of this material from Okinawa Island with the other specimens from temperate Japanese waters disclosed that the former was distinct from the three species of Pagurus referred to P. pilosipes by previous authors, and also from P. insulae. Additionally, none of the three Pagurus species or P. insulae has been collected in the Ryukyu Islands during field investigations by the author since 1994. Therefore, I came to the conclusion that the four topotypic specimens from Okinawa Island represented the true P. pilosipes. A neotype is selected from the topotypic specimens for P. pilosipes in the interest of nomenclatural stability. The close similarities

among P. pilosipes, three species mistakenly identified as P. pilosipes and P. insulae led the author to reexamine the type series of P. insulae for detailed comparison. It was found that the original description by Asakura (1991) omitted morphological variations in shape and armature of the right cheliped and armature of the left third pereopod, which make most of the distinguishing characters proposed by him unreliable. Further, Asakura's illustrations are not consistent in many details with the actual specimens used by him for drawings, for example shape of the antennal acicle, structures of the mouthparts, armature of the right cheliped. and setation of the telson. In this paper, P. *pilosipes* is fully redescribed and three new species of Pagurus, P. erythrogrammus, P. quinquelineatus, P. nigrivittatus are described. A supplemental description and full illustrations are given for P. insulae for completeness. Distinguishing characters among the five species are discussed.

Materials and Methods

The specimens examined in this study are deposited in the following institutions: Natural History Museum and Institute, Chiba (CBM, with a code of ZC); Coastal Branch of Natural History Museum and Institute, Chiba, Katsuura (CMNH, with a code of ZC); National Science Museum, Tokyo (NSMT, with a code of Cr); Osaka Museum of Natural History (OMNH, with a code of Ar); Showa Memorial Institute, National Science Museum, Tsukuba (NSMT-R, with a code of Cr); National Taiwan Ocean University, Keelung, Taiwan, R.O.C. (NTOU); Muséum national d'Histoire naturelle, Paris (MNHN, with a code of Pg); National Museum of Natural History, Smithsonian Institution (USNM); Zoological Laboratory, Faculty of Agriculture, Kyushu University (ZLKU) (now housed in the Kitakyushu Museum of Natural History and Human History). The shield length, abbreviated as sl, is measured from the tip of rostrum to the midpoint of posterior margin of the shield. For detailed observation of the surface structure on the integument, the specimens (including removed appendages) were stained with methylene blue solution. The terminology used in

the description follows generally that of McLaughlin (1974), with exception of the posterior carapace (see Lemaitre, 1995), fourth pereopod (see McLaughlin, 1997), gill structure (see McLaughlin and de Saint Laurent, 1998), paragastric grooves on the shield (Komai and Osawa, 2001), dactylus (dactyli) for dactyl (dactyls), and numbered thoracic sternites. The drawings were made with the aid of a drawing tube mounted on a Leica MZ 8 stereomicroscope.

Taxonomic Account

Pagurus pilosipes (Stimpson, 1858) (Figs. 1–5, 24A)

- *Eupagurus pilosipes* Stimpson, 1858: 249 (87) [type locality: Loo Choo (=Okinawa Island)]; Alcock, 1905: 177; Stimpson, 1907: 223; Terao, 1913: 371; Gordan, 1956: 333.
- ?Not *Pagurus pilosipes*—Wang, 1992: 61; 1994: 570. See "Discussion."
- Not *Pagurus pilosipes*—Miyake, 1978; 91, fig. 34. See "Discussion."
- Not *Pagurus pilosipes*—Miyake and Imafuku, 1980: 60, pl. 2, fig. 5; Miyake, 1982: 132, pl. 44, fig. 5; Oh, 1983: 101 (key), 106, pl. 1, figs. 3, 4, pl. 2, figs. 1–5; Takeda, 1986: 124, unnumbered fig.; Asakura, 1991: 798; Miyake, 1991: 132, pl. 44, fig. 5; Asakura, 1995: pl. 97, fig. 9, 363; Miyake, 1998: 132, pl. 44, fig. 5; Minemizu, 2000: 148, unnumbered fig. [=*Pagurus nigrivittatus* sp. nov.] See "Discussion."

Material examined. Neotype. Heshikiya, Katsuren, Okinawa Island, lower intertidal, on small colony of *Pociropora* sp., 23 June 1994, hand, coll. T. Komai, 1 female (sl 2.5 mm) (CBM-ZC 6383).

Other material. Same data as for neotype, 1 male (sl 1.9 mm), 2 females (sl 2.2, 2.4 mm) (CBM-ZC 6384).

Redescription. Eleven pairs of biserial phyllobranchiae.

Shield (Fig. 1A) 1.0–1.1 times as long as broad; rostrum broadly triangular, terminating subacutely, slightly overreaching lateral projections, with tuft of short setae basally; lateral projections obtusely triangular, with small submarginal spine; anterior margin between rostrum and lateral projections concave; anterolateral margins sloping; posterior margin roundly truncate; dorsal surface weakly convex, with several pairs of tufts of short setae laterally and 1 median tuft of setae on gastric region; paragstric grooves rather conspicuous. Posterior carapace (Fig. 1B) generally membranous except for weakly calcified anterior part of posteromedian plate, with paired tufts of short to moderately long setae and several low blister-like tubercles on submedian part; cardiac sulci nearly subparallel, reaching beyond midlength of posterior carapace; sulci cardiobranchialis very short.

Ocular peduncles (Fig. 1A) relatively slender, about 0.8 of shield length, weakly inflated basally, each with 2 rows of short setae on dorsomesial face; cornea slightly inflated, maximal diameter subequal to basal diameter of peduncle. Ocular acicles (Fig. 1A) moderately separated basally, subovate, each with submarginal terminal spine; dorsal surface slightly concave. Interocular lobe (Fig. 1 A) clearly visible in dorsal view, with concave anterior surface.

Antennular peduncles (Fig. 1A), when fully extended, overreaching corneas by 0.1–0.2 length of ultimate segment. Ultimate segment 1.4–1.6 times as long as penultimate segment, weakly widened distally in lateral view. Basal segment unarmed on lateral face of statocyst lobe.

Antennal peduncles (Fig. 1A) not reaching corneas. Fifth and fourth segmens with few tufts of short setae. Third segment with small spine at ventromesial distal angle. Second segment with dorsolateral distal angle produced, reaching to midlength of fourth segment, terminating in simple or bifid spine, dorsomesial distal angle with small but distinct spine. First segment with spinule on lateral face distally, ventromesial distal margin with 1 or 2 spinules laterad of strongly produced antennal gland opening. Antennal acicle arcuate, reaching base of cornea, terminating in sharp spine; mesial margin with row of sparse tufts of short to moderately short setae.

Mandible (not illustrated) without distinctive characters. Endopod of maxillule (Fig. 2 A) with recurved outer lobe. Maxilla, first and second maxillipeds as illustrated (Fig.



Fig. 1. *Pagurus pilosipes* (Stimpson, 1858). A, shield and cephalic appendages, dorsal; B, carapace, dorsal; C, left fourth pereopod, lateral; D, coxae of fifth pereopods and eighth thoracic sternite, ventral; E, anterior lobe of sixth thoracic sternite, ventral; F, telson, dorsal. A–C, E, F, neotype female (sl 2.5 mm; CBM-ZC 6383); D, male (sl 1.9 mm; CBM-ZC 6384).

2B–D). Third maxilliped (Fig. 2E) with moderately stout endopod; propodus moderately stout; carpus without dorsodistal spine; merus with dorsodistal and ventromesial spines; ischium (Fig. 2F) with well-developed crista dentata and with 1 accessory tooth; basis (Fig. 2F) with 1 or 2 small teeth on mesial margin; exopod distinctly overreaching distal margin of merus.

Right cheliped (Fig. 3A-D) larger than left



Fig. 2. *Pagurus pilosipes* (Stimpson, 1858). Left mouthparts. A, maxillule, ventral; inset, endopod, lateral; B, maxilla, ventral; C, first maxilliped, ventral; D, second maxilliped, ventral; E, third maxilliped, lateral; F, ischium and basis of third maxilliped, dorsal. Neotype female (sl 2.5 mm; CBM-ZC 6383).

cheliped. Chela subtriangular in dorsal view; fingers not strongly depressed dorsoventrally; no distinct hiatus between fingers. Dactylus slightly shorter than palm; dorsal surface with tufts of setae and row of small spines mesiad of dorsal midline, dorsomesial margin distinctly delimited by row of small spines; mesial and ventral faces unarmed, but with row of tufts of setae; cutting edge with row of calcareous teeth in proximal 0.7 and row of small corneous teeth in distal 0.3, terminating in small corneous claw. Palm shorter than carpus; dorsal surface convex, with rather widely-spaced, moderately large spines arranged in 5 or 6 irregular rows (lateral rows extending onto fixed finger) and numerous tufts of long setae; dorsolateral and dorsomesial margins each delimited by row of moderately large spines; lateral face with scattered, bifid or multifid small protuberances; mesial face with row of tiny tubercles adjacent to dorsomesial margin and few tufts of setae; ventral surface weakly inflated, with few low protuberances and scattered tufts of long setae. Cutting edge of fixed finger with row of calcareous teeth (1 tooth at midlength prominent), terminating in small corneous claw. Carpus shorter than merus, noticeably widened distally in dorsal view; dorsal surface without delineation of dorsolateral margin, with several spines (3 spines adjacent to dorsomesial margin partic-





Fig. 3. *Pagurus pilosipes* (Stimpson, 1858). Right cheliped. A, chela, dorsal (setae omitted); B, carpus, dorsal (setae omitted); C, entire cheliped, lateral; D, same, mesial (setae omitted). Neotype female (sl 2.5 mm; CBM-ZC 6383).

ularly large), low protuberances having denticulate anterior margins, and tufts of long setae; dorsomesial margin distinctly delimited by row of large spines decreasing in size proximally; dorsodistal margin with row of small to moderately large spines; lateral face with short denticulate ridges and tufts of long setae, ventrolateral margin with row of small spines distally; mesial face unarmed, but with few setae; ventral surface weakly inflated, with few setae. Merus with row of tufts of setae on dorsal surface, dorsodistal margin with 2 or 3 spines; lateral face with very short, low ridges, ventrolateral margin with row of moderately large spines and tufts of long setae distally; mesial face with oblique short ridges adjacent to ventromesial margin, but otherwise smooth, ventromesial margin with 3 or 4 spines increasing in size proximally; ventral surface produced ventrally in lateral part, but lacking prominent tubercle, with scattered tufts of long setae. Ischium with few tufts of setae on dorsal and ventral surfaces; ventromesial margin with row of tiny spines or tubercles.

Left cheliped (Fig. 4A-C) reaching base to midlength of dactylus of right cheliped. Chela subovate in dorsal view; no hiatus between fingers. Dactylus distinctly longer, but not exceeding twice length of palm; dorsal surface with short row of small spines on midline and tufts of short to moderately long setae, dorsomesial margin not delimited; mesial face with few tiny tubercles proximally and tufts of setae; cutting edge with fine row of small corneous teeth. Palm distinctly shorter than carpus; dorsal surface somewhat elevated in midline, but not crested, with 2 irregular rows of moderately large spines extending onto fixed finger, mesial part with few small tubercles or spines; numerous scattered tufts of long setae on entire dorsal surface of palm and fixed finger; dorsolateral margin clearly delimited by row of small spines; dorsomesial margin weakly delimited by row of small spines or tubercles; lateral face with several low tubercles or protuberances and tufts of short setae; mesial face unarmed, but with tufts of setae; ventral surface nearly smooth, with scattered tufts of long setae. Cutting edge of fixed finger with row of minute calcareous teeth in proximal 0.8, terminating in small corneous claw. Carpus moderately compressed laterally, somewhat widened distally in dorsal view; dorsolateral and dorsomesial margins each with row of spines increasing in size distally and tufts of long setae, surface between margins unarmed; lateral face with spinulose tubercles and low, occasionally bifid or multifid protuberances, and with tufts of short to moderately short setae, ventrolateral margin with row of moderately large spines; mesial face dorsally with large, but low protuberances bearing setae and ventrally with few tufts of setae, ventromesial distal margin unarmed; ventral surface weakly inflated, with tufts of long setae. Merus with row of short transverse ridges and moderately long setae on dorsal surface, dorsodistal margin unarmed; lateral face with few, very short, low ridges dorsally and ventrally, ventrolateral margin with 6 or 7 large spines; mesial face smooth, with few short vertical rows of setae, with 3 large spines; ventral surface concave, with scattered tufts of long setae. Ischium with row of small spines or tubercles on ventromesial margin.

Second and third pereopods (Fig. 5A, C) generally similar, moderately slender, with rather sparse rows of tufts of moderately long setae on dorsal and ventral surfaces of each segment. Dactyli 1.0-1.1 times as long as propodi, weakly curved in lateral view, not twisted in dorsal view; lateral and mesial faces each with few setae; mesial faces unarmed or with 1 spinule proximal to base of claw on second (Fig. 5B), with few corneous spinules adjacent to dorsal margin in distal half on third (Fig. 5D); ventral margins each with 6 or 7 long corneous spines. Propodi distinctly longer than carpi, slightly curved ventrally, unarmed on dorsal surfaces; lateral faces devoid of rows of calcareous spines or tubercles on left third pereopod; ventral surfaces not tuberculate, each with row of 3 or 4 small corneous spines on distal half (distalmost spine shorter than distal spines on dactylus on left third pereopod). Carpi each only with dorsodistal spine on dorsal surface; lateral faces each with some tufts of moderately short setae dorsally. Meri each with nearly smooth dorsal margins; lateral faces naked; ventral margins with row of small spines or



Fig. 4. *Pagurus pilosipes* (Stimpson, 1858). Left cheliped. A, chela and carpus, dorsal (setae omitted); B, entire cheliped, mesial (setae omitted); C, same, lateral. Neotype female (sl 2.5 mm; CBM-ZC 6383).

tubercles in second, smooth in third, no spinule at ventrolateral distal margins. Paired gonopores on third pereopods in females.

Fourth pereopods (Fig. 1C) similar from left to right in structure, semichelate, with tufts of long setae on dorsal surfaces of propodus to merus and ventral margin of merus. Dactylus terminating in strongly curved corneous claw, ventral margin with row of small corneous teeth increasing in size distally; no preungual process. Propodus moderately deep with notably convex ventral margin, rasp composed of 3 or 4 rows of corneous scales.

Fifth percopods chelate; paired gonopores in males (Fig. 1D).

Anterior lobe of sixth thoracic sternite (Fig. 1E) subrectangular, with sparse setae on anterior margin. Eighth thoracic sternite (Fig. 1D) with 2 narrowly separated, rounded lobes, each with sparse short setae on anterior margin.

Abdomen twisted; 3 unpaired left pleopods in males, 4 unpaired left pleopods in females.

Telson (Fig. 1F) with distinct transverse indentations; anterior lobe with row of long setae on convex lateral margins; lateral margins of posterior lobes convex or sinuous, with few setae; median cleft very small, terminal margins weakly oblique, each with 4 or 5 large spines.

Coloration in formalin. Shield mottled with

Reassessment of Pagurus pilosipes



Fig. 5. *Pagurus pilosipes* (Stimpson, 1858). A, right second pereopod, lateral; B, dactylus of right second pereopod, mesial (setae omitted); C, left third pereopod, lateral; D, dactylus of left third pereopod, mesial (setae omitted). Neotype female (sl 2.5 mm; CBM-ZC 6383).

brown and cream. Ocular peduncles generally light brown, distal part darker, without distinct transverse bands or longitudinal stripes. Antennular and antennal peduncles light brown. Right chela generally right brown; dactylus with 2 reddish brown stripes (one between dorsomesial rows of spines and shorter one on mesial face proximally); spines on dorsal surface (including those on dorsolateral margin) whitish; mesial face of palm with dark brown patch; carpus with 3 dark brown stripes on dorsal surface (lateral 2 stripes broad, rather obscurely defined, and mesial stripe along dorsomesial margin); mesial face of carpus with 1 dark brown stripe medially; ventromesial face of carpus dark brown; merus mottled with irregular pattern of dark brown and cream. Second and third pereopods (Fig. 24A) generally light yellowish brown longitudinally striped by reddish brown; dactyli each with 3 stripes on lateral face; propodi each with 4 stripes visible in lateral view, dorsal and ventral surfaces without stripe; carpi each with 3 lateral stripes; meri each with 3 lateral stripes and occasionally with indistinct patch of reddish brown proximoventrally.

Size. Male sl 1.9 mm, females sl 2.2–2.5 mm.

Distribution and habitat. So far known only from Okinawa Island, Ryukyu Islands; lower intertidal. The specimens used gastropod shells for microhabitat, and inhabited on a small colony of a live coral *Pociropora* sp. on sand flat area.

Pagurus insulae Asakura, 1991 (Figs. 6–11, 24E)

Pagurus insulae Asakura, 1991: 793, figs. 1, 2; Asakura et al., 1993: 5, fig. 3; Asakura, 1995: pl. 97, fig. 8, 363; Komai, 1999: 2 (list).

Material examined. Holotype. Chichi-jima Island, Ogasawara Islands, intertidal, 1986 and 1989 (no exact date given), hand, coll. A. Asakura, male (sl 3.4 mm) (CBM-ZC 711).

Paratypes. Okumura, Sakaiura and Toufuiwa on Chichi-jima Island, intertidal, 1986 and 1989 (no exact date was given), hand, coll. A. Asakura, 15 males (sl 1.6–3.4 mm), 6 females (sl 1.8–2.6 mm), 4 ovigerous females (sl 2.0–2.5 mm) (CBM-ZC 712).

Other material. Miyanohama Beach, Chichijima Island, intertidal, 15 October 1997, hand, coll. T. Komai, 1 male (sl 3.3 mm) (CBM-ZC 6480); same locality, intertidal, 16 June 1995, hand, coll. M. Osawa, 1 female (sl 2.3 mm) (NSMT-Cr 15147); Kopepe Beach, Chichi-jima Island, intertidal, 25 September 2000, hand, coll. M. Osawa, 1 male (sl 2.5 mm) (NSMT-Cr 15148).

Supplemental description. Eleven pairs of biserial phyllobranchiae.

Rostrum (Fig. 6A) triangular, terminating subacutely or acutely, exceeding lateral projections, but not reaching anterior margin of interocular lobe; dorsal surface of shield (Fig. 6A) slightly convex, with some pairs of tufts of short to moderately long setae laterally and 1 median tuft of setae; paragastric grooves inconspicuous. Posterior carapace (Fig. 6B) membranous except for weakly calcified anterior part of posteromedian plate, with paired tufts of moderately short setae; cardiac sulci slightly diverging posteriorly, reaching beyond midlength of posterior carapace; sulci cardiobranchialis short, but occasionally reaching to midlength of posterior carapace.

Ocular peduncles (Fig. 6A) moderately stout, 0.6–0.8 of shield length; corneas slightly inflated, maximal diameter slightly greater than basal diameter of ocular peduncle. Interocular lobe (Fig. 6A) visible in dorsal view, with slightly concave anterior surface.

Antennular peduncles (Fig. 6A), when fully extended, overreaching cornea by 0.1–0.2 length of ultimate segment. Ultimate segment 1.4–1.5 times as long as penultimate segment, somewhat widened distally in lateral view, with few short setae on dorsal surface. Basal segment unarmed on lateral face or distolateral margin of statocyst lobe.

Antennal peduncles (Fig. 6A) not reaching or reaching corneas. First segment with small spine laterad of antennal gland opening on ventromesial distal margin. Antennal acicle moderately slender, arcuate, reaching beyond base of cornea, but not reaching distal margin of cornea, with row of stiff setae on mesial margin. Antennal flagellum long, distinctly overreaching fully extended right cheliped.

Mouthparts (Fig. 7A-F) as illustrated. Endopod of maxillule (Fig. 7B) with weakly produced inner lobe, outer lobe obsolete. Third maxilliped (Fig. 7F) with moderately stout to stout endopod; propodus occasionally notably thickened in males; carpus without dorsodistal spine; merus unarmed on dorsodistal and ventromesial margins; ischium (Fig. 15G) with crista dentata composed of fine row of small corneous teeth, 1 accessory tooth present; basis (Fig. 7G) with 1 or 2 small tooth on mesial margin; exopod reaching or slightly overreaching distal margin of merus.

In males (sl 2.5–3.4 mm), right cheliped (Fig. 8A-C) showing tendency toward elongation with increase of body size. Chela generally subovate in dorsal view, twice length of greatest width; fingers somewhat depressed dorsoventrally, with prominent hiatus. Dactylus distinctly shorter than palm; dorsal surface with row of moderately small spines adjacent to dorsomesial margin; dorsomesial margin distinctly delimited by row of numerous small spines and tufts of moderately short setae; mesial face with irregular row of spines adjacent to dorsomesial margin; ventral surface with rows of tufts of setae; cut-



Fig. 6. *Pagurus insulae* Asakura, 1991. A, shield and cephalic appendages, dorsal; B, carapace, dorsal (setae on shield omitted); C, left fourth pereopod, lateral; D, coxae of fifth pereopods and eighth thoracic sternite, ventral; E, anterior lobe of sixth thoracic sternite; F, telson, dorsal; G, terminal margins of telson, posterodorsal. Holotype male (sl 3.4 mm; CBM-ZC 711).

ting edge with row of calcareous teeth, terminating in small corneous claw. Palm slightly shorter than carpus; dorsal surface slightly convex, without delineation of dorsomesial margin, covered with numerous small spines (generally increasing in size distally), spinulose tubercles and granules extending onto fixed finger, and with rather sparse short to long setae; dorsolateral margin delimited by row of small spines increasing in size distally;



Fig. 7. *Pagurus insulae* Asakura, 1991. Mouthparts. A, right mandible, dorsal; B, right maxillule, ventral; inset, endopod, lateral; C, right maxilla, ventral; D, right first maxilliped, ventral; E, left second pereopod, ventral; F, left third maxilliped, lateral; G, ischium and basis of left third maxilliped, dorsal. Holotype male (sl 3.4 mm; CBM-ZC 711).

lateral face covered with small, rounded tubercles occasionally forming short obliquely vertical rows and few short setae; mesial face densely covered with small spines or tubercles and few short setae; ventral surface weakly convex, with some low protuberances and short setae. Carpus about 1.6 times longer than distal width, subequal in length to merus; dorsal surface covered with small spines and tubercles, occasionally arranged in short to moderately short transverse rows, and rather sparse tufts of moderately short setae; dorsolateral and dorsomesial margins not delimited; lateral face covered with small, low tubercles occasionally arranged in short obliquely vertical rows and with few short setae, ventrolateral distal margin with row of small spines; mesial face covered with small spines and low, simple or bifid tubercles, and also with short denticulate ridges proximally; ventral surface inflated, with numerous low tubercles and few short setae. Merus with row of short transverse ridges each bearing moderately short setae on dorsal surface, distalmost ridge denticulate, extending onto lateral and mesial



Fig. 8. *Pagurus insulae* Asakura, 1991. Right cheliped. A, chela and carpus, dorsal (setae omitted); B, entire cheliped, mesial; C, same, lateral. Holotype male (sl 3.4 mm; CBM-ZC 711).

faces; dorsodistal margin with row of small denticles; lateral face with scattered, small, low tubercles and tufts of short setae, ventrolateral margin with row of small spines in distal half; mesial face with some tufts of short setae dorsally and short denticulate ridges or low tubercles ventrally, ventromesial margin with row of small, sharp or blunt spines; ventral surface with some low tubercles and sparse setae, but without prominent T. Komai



Fig. 9. *Pagurus insulae* Asakura, 1991. Right cheliped. A, chela, dorsal (setae omitted); B, carpus, dorsal (setae omitted); C, entire cheliped, lateral (setae omitted); D, same, mesial. Paratype female (sl 2.6 mm; CBM-ZC 712).

tubercle. Ischium with short to moderately short setae on every surface; ventromesial margin with row of spinules; ventrolateral margin also with row of tiny spines.

In females and small males (sl 1.6-1.7 mm), right cheliped (Fig. 9A-D) not particularly elongate. Chela subtriangular in dorsal view, 1.3-1.4 times as long as wide; no distinct hiatus between fingers. Dactylus longer than palm; dorsal surface with tufts of long setae and several small spines, those adjacent to dorsomesial margin occasionally forming inconspicuous row; dorsomesial margin clearly delimited by row of small spines; mesial face unarmed, but with tufts of moderately long setae; cutting edge with small calcareous teeth in proximal 0.6 and fine row of rather long corneous teeth in distal 0.4, terminating in large corneous claw. Palm distinctly shorter than carpus, dorsal surface weakly convex, with numerous (but not extremely dense) small spines arranged in 7 or 8 irregular rows and tufts of long setae; dorsolateral margin delimited by row of large spines; dorsomesial margin clearly delimited by row of small, occasionally blunt spines; lateral face with low, simple or bifid tubercles and few setae; mesial face with few low protuberances dorsally and tufts of setae; ventral surface slightly convex, with few low protuberances and tufts of long setae. Carpus only slightly longer than distal width; dorsal surface with numerous, scattered, small to large spines and tufts of long setae; dorsomesial margin delimited by row of large spines; lateral face with scattered small, low tubercles, ventrolateral distal margin with row of small spines; mesial face with simple or bifid, low protuberances adjacent to dorsomesial margin, ventromesial distal margin with row of blunt spines; ventral surface strongly convex, with some low protuberances and long setae. Merus with short transverse ridges on dorsal surface, dorsodistal margin denticulate; lateral face with small, low tubercles occasionally forming short rows; ventrolateral margin with row of spines increasing in size distally; mesial face nearly smooth except for few low protuberances adjacent to ventromesial margin, ventromesial margin with row of small spines; ventral surface with large tubercle. Ischium with sparse, tiny tubercles on ventromesial margin; ventrolateral margin unarmed.

Left cheliped (Fig. 10A-E) more slender in males than in females. Chela subovate in dorsal view, 2.0-2.1 times as long as wide in males, 1.8-1.9 times as wide in females; prominent hiatus between fingers in males, but no hiatus in females. Dactylus distinctly longer than palm; dorsal surface with some small spines proximally and tufts of short to moderately long setae, dorsomesial margin not delimited; mesial face with few tiny tubercles proximally and tufts of long setae; ventral surface with tufts of long setae; cutting edge with row of small corneous teeth in males, with row of small calcareous teeth in proximal 0.6 and row of small corneous teeth in distal 0.4 in females. Palm distinctly shorter than carpus; dorsal surface somewhat elevated in midline, but not crested, with 4 or 5 rows of spines extending onto fixed finger (spines on 2 median rows larger than others); mesial part of dorsal surface with few tiny tubercles or low protuberances; numerous tufts of long setae scattered on dorsal surface of palm including fixed finger; lateral margin not clearly delimited in males, weakly delimited by row of small tubercles in females; dorsomesial margin not clearly delimited; mesial face with few low protuberances and short setae; ventral surface slightly convex, with tufts of long setae. Cutting edge of fixed finger with row of small corneous teeth in distal 0.4-0.6. Carpus somewhat compressed laterally, slightly widened distally in dorsal view; dorsolateral and dorsomesial margins each delimited by row of spines increasing in size distally and tufts of long setae (spines larger in females than in males), surface between margins unarmed; lateral face with low, occasionally bifid or multifid tubercles, and with few setae, ventrolateral margin with row of small tubercles; mesial face with few low protuberances and tufts of long setae, ventromesial distal margin smooth; ventral surface weakly inflated, with tufts of long setae. Merus with row of short transverse and moderately short setae on dorsal surface, dorsodistal margin unarmed; lateral face with tiny low tubercles or low protuberances and few short setae, ventrolateral



Fig. 10. *Pagurus insulae* Asakura, 1991. Left chelipeds. A, chela and carpus, dorsal (setae omitted); B, E, entire chelipeds, lateral (setae omitted); C, entire cheliped, mesial; D, chela, dorsal (setae omitted). A-C, holotype male (sl 3.4 mm; CBM-ZC 711); D, E, paratype female (sl 2.6 mm; CBM-ZC 712).

margin with 5–7 moderately small spines; mesial face almost smooth, with few short ridges ventrally, ventromesial margin with row of small spines; ventral surface with very large tubercle occasionally directed posteriorly (sometimes greatly reduced in males), and with scattered tufts of long setae. Ischium with row of small spines on ventromesial margin; tufts of long setae on lateral and ventral surfaces.



Fig. 11. *Pagurus insulae* Asakura, 1991. A, right second pereopod, lateral; B, dactylus of right second pereopod, mesial (only mesial setae illustrated); C, left third pereopod, lateral; D, dactylus of left third pereopod, mesial (only mesial setae illustrated); E, dactylus and propodus of left third pereopod, lateral. A-D, holotype male (sl 3.4 mm; CBM-ZC 711); E, paratype female (sl 2.6 mm; CBM-ZC 712).

Second pereopods (Fig. 11A) showing tendency toward elongation in males; row of tufts of moderately short to long setae present on dorsal and ventral surfaces of each segment. Dactyli 0.9-1.1 times as long as propodi; lateral faces each with shallow median sulcus and rows of tufts of long setae dorsally and ventrally; mesial faces (Fig. 11B) each with row of corneous spinules dorsally and row of tufts of long setae ventrally; ventral margins each with 7-12 moderately short corneous spines. Propodi unarmed on dorsal surfaces; lateral and mesial faces with rows of tufts of long setae dorsally and ventrally; ventral surfaces not tuberculate, with row of 3 or 4 short corneous spines in distal half. Carpi each with only dorsodistal spine on dorsal surface. Meri with ventral margins each bearing row of small spines or low protuberances, ventrolateral distal margin with some spinules.

Third pereopods (Fig. 11C, E) dissimilar from right to left in both sexes. Dactyli 1.0-1.1 times as long as propodi; dorsal surfaces unarmed; lateral faces smooth on right or bearing short rows of small calcareous tubercles ventrally on left (tubercles sometimes reduced in males); mesial faces (Fig. 11D) each with row of widely-spaced corneous spinules on either side of shallow median sulcus; ventral margins each with 9-13 moderately short corneous spines. Propodi moderately slender in males, stout in females, lateral faces smooth (right) or bearing rows of small calcareous tubercles ventrally (left; tubercles occasionally reduced in males); ventral surfaces only slightly tuberculate (right) or slightly to somewhat tuberculate or denticulate, terminating distally in small spine (left), with row of 3 or 4 short corneous spines mesially (distalmost spine shorter than distal spines on dactylus).

Fourth percopods (cf. Fig. 6C) semichelate, generally similar to right to left; dorsal surfaces of propodi, carpi and meri and ventral surfaces of meri with numerous long setae. Propodus moderately deep with convex ventral margin, rasp consisting of 5 or 6 rows of corneous scales; mesial face flat.

Fifth pereopods with paired gonopores in males (Fig. 6D), left gonopore partially obscured by tufts of setae.

Anterior lobe of sixth thoracic sternite (Fig. 6E) subsemicircular, slightly skewed to left, with numerous long setae on anterior surface. Eighth thoracic sternite (Fig. 6D) with 2 rounded lobes moderately separated and somewhat produced ventrolaterally, each with numerous setae anterolaterally.

Telson (Fig. 6F) with deep transverse indentations; median cleft small; terminal margins slightly oblique or concave, with row of 12–14 spinules (2–4 spinules at outer angle calcareous, larger than other corneous spinules) (Fig. 6G).

Color in life. Shield light gray, with faint dark brown markings laterally. Right cheliped generally dark gray-brown; distal part of dactylus whitish; spines on dorsal surface and low protuberances on ventral surface paler; carpus with white longitudinal stripe on dorsal surface mesially; spines comprising dorsomesial rows of carpus dark gray-brown, while spines on dorsal surface whitish; darker, irregularly spotted markings on lateral and mesial faces of carpus; merus with white transverse band subdistally, dark graybrown area on lateral and mesial faces irregularly spotted by white. Color pattern of left cheliped generally similar to that of right, but marking on mesial face of carpus forming clear stripe. Ambulatory legs generally white with distinct dark gray-brown stripes; dactyli with dorsal and ventral surfaces dark gray-brown, lateral and mesial faces each with median stripe; propodi and carpi with white dorsal and dark gray-brown ventral surfaces, lateral and mesial faces each with 2 distinct stripes (1 dorsal and 1 median); dorsal stripes on lateral faces of propodi usually reaching distal end (cf. Fig. 24E); meri each with 3 stripes on lateral face (middle and ventral stripes occasionally connected distally).

Size. Males sl 1.6-3.4 mm; females sl 1.8-2.6 mm, ovigerous females sl 2.0-2.5 mm.

Variations. As is apparent from the above description, great morphological variations are observed in the length and armature of the right cheliped, armature of the merus of the left cheliped and dissimilarity of ornamentation on the third percopods. The right cheliped is notably elongate in the three relatively large males (sl 3.3–3.4 mm). The dorsal

surfaces of the right palm and carpus are densely covered with small spines or tubercles, but with few tufts of setae in 13 males (sl 2.5-3.4 mm), while it bears larger spines arranged in seven or eight irregular rows and numerous tufts of longer setae in all females and three small males (sl 1.6-1.7 mm). The ventral tubercles on the meri of the chelipeds are constantly well-developed in females, but they show a tendency toward reduction with increase of the body size in males. In the three small males (sl 1.6-1.7 mm), the ventral tubercles on the meri of the chelipeds are well developed as in females, but they are rudimentary in 11 larger males (sl 2.6-3.0 mm); in the three largest specimens (sl 3.3-3.4 mm), the meral tubercles are completely absent. The ventrolateral rows of small calcareous tubercles are present on the lateral surface of the propodus of the left third pereopod in all females and three small males, but absent or greatly reduced in other 11 males.

Notable thickening of the propodus of the third maxilliped is observed in five males (sl 2.8-3.4 mm).

Distribution. So far known only from Chichijima Island, Ogasawara Islands; intertidal to subtidal. Found to use gastropod shells for microhabitat (Asakura, 1991).

Remarks. In the original description of *P*. insulae, Asakura (1991) compared the species with P. filholi (as P. geminus McLaughlin, 1976) and a species believed at that time to represent P. pilosipes (=P. nigrivittatus sp.nov.; see "Discussion"). He considered that the armature and setation of the chelipeds, ornamentation of the left third pereopod and coloration in life provided diagnostic features in discriminating P. insulae from the two relatives. During this study, however, it has been found that intraspecific variations in morphology of the chelipeds and ambulatory percopods were not considered in the original description of P. insulae. The characters proposed by Asakura (1991) in distinguishing P. insulae from P. nigrivittatus sp. nov., i.e. the dorsal armature and setation of the right palm, the development of the ventral tubercles on the cheliped meri, and the presence or absence of the ventrolateral rows of calcareous tubercles on the propodus of the left third percopod are subject to considerable variation in both *P. insulae* and *P. nigrivittatus* (see "Variations" under account of respective species). Additionally, Asakura (1991) noted in "Remarks" section that the stripes on the ambulatory legs are more reddish in *P. insulae* than in *P. nigrivittatus* sp. nov. (as *P. pilosipes*), although he described the stripes as being dark brown in "Coloration" section. It has been found that, in fact, the stripes on the ambulatory legs are similarly dark brown in life in the two species. As discussed later, there are some other differences which warrant full specific status for *P. insulae* and *P. nigrivittatus* sp. nov.

Inconsistency is found between the specimens used by Asakura (1991) for preparation of drawings and the given illustrations. For example, the armature on the chela and carpus of the right cheliped of the holotype figured by Asakura (1991, fig. 1b) is considerably different from that actually observed on the holotype. The spines on the right palm and carpus are much smaller and more numerous in the holotype than those illustrated. The antennal acicles are actually longer and more slender in the holotype than those illustrated. According to Asakura's (1991) illustration (Fig. 2b), there is no trace of the inner lobe on the maxillule endopod and the distal part of the endopod bears three setae. However, in fact, the inner lobe is weakly produced with one apical bristle; there are no setae on the distal part. The crista dentata of the third maxilliped is fine, unlike that illustrated. Many spiniform setae on the telson are illustrated by Asakura (1991, fig. 1f). However, there are no such numerous spiniform setae on the telson in the holotype.

Pagurus erythrogrammus sp. nov. (Figs. 12–15, 24C, 25A)

Pagurus pilosipes—Miyake, 1978: 91 (part), fig. 34a. Not Pagurus pilosipes (Stimpson, 1858).

Material examined. Holotype. Sea of Japan: Takasa, Echizen, Fukui Prefecture, 2 m, 29 May 2001, SCUBA diving, coll. T. Sugimoto, male (sl 3.3 mm) (CBM-ZC 6495).

Paratypes. Japan Boso Peninsula: Ashikane, off Kamogawa, 20 m, 18 Oct 1995, SCUBA, coll. J. Okuno, 1 female (sl 2.2 mm) (CBM-ZC 6498); Hasama Beach, Tateyama, Boso Peninsula, intertidal, 2 May 1996, hand, coll. T. Komai, 1 male (sl 2.3 mm), 3 ovigerous females (sl 1.8-2.2 mm) (CBM-ZC 6496); Hasama Beach, Tateyama, 16 May 1996, hand, coll. T. Komai, 3 males (sl 2.3-2.9 mm), 1 female (sl 2.0 mm) (CBM-ZC 6497); same data, 1 male (sl 3.0 mm) (MNHN-Pg); Igai-jima Islet, Kamogawa, 16 m, 24 June 2001, SCUBA, coll. J. Okuno, 1 male (sl 4.0 mm) (CMNH-ZC 628); Hatto-ne, off Kamogawa, 15 m, 26 November 2000, SCUBA, coll. J. Okuno, 1 male (sl 2.1 mm) (CMNH-ZC 1010); same data, 1 male (sl 2.1 mm), 1 female (sl 2.1 mm) (CMNH-ZC 1011); Ashika-ne, off Kamogawa, 26 m, 26 November 2000, SCUBA, coll. J. Okuno, 1 male (sl 2.5 mm) (CMNH-ZC 1012); Okinoshima, Tateyama, 5.5 m, 28 June 2002, SCUBA, 1 ovigerous female (sl 1.6 mm) (CMNH-ZC 1013). Sagami Bay: Kamegi-sho, 14 m, 24 July 1960, dredge, 1 male (sl 3.4 mm), Miyake (1978) det. no. 385 (NSMT-CrR 1803); same data, 1 male (sl 2.2 mm), 1 ovig (sl 1.9 mm), Miyake (1978) det. no. 388 (NSMT-CrR 1806); same locality, 16 m, 28 July 1960, dredge, 1 ovigerous female (sl 2.2 mm), Miyake (1978) det. no. 408 (NSMT-CrR 1826); same locality, 25 July 1960, dredge, 1 male (sl 1.6 mm), Miyake (1978) det. no. 409 (NSMT-CrR 1827); same locality, 28 July 1960, dredge, 1 male (sl 3.2 mm), Miyake (1978) det. no. 411 (NSMT-CrR 1829); similar locality, 14 m, 25 July 1960, dredge, 1 male (sl 3.6 mm), Miyake det. no. 416 (NSMT-CrR 1834); 2 km off west north-by-west of Jogashima Islet, 57-75 m, 3 February 1962, dredge, 1 ovig (sl 2.1 mm), Miyake (1978) det. no. 455 (NSMT-CrR 1965); Futo, Izu Peninsula, 10 m, 1995, SCUBA, coll. M. Mitsuhashi, 2 males (sl 1.5, 1.7 mm) (CBM-ZC 6499); Yahatano, Izu Peninsula, 2 m, 12 July 1998, SCUBA, coll. M. Mitsuhashi, 1 female (sl 2.5 mm). Kii Peninsula: Sabiura, Kushimoto, 5-10 m, December 1994, SCUBA, coll. K. Nomura, 1 male (sl 2.9 mm) (CBM-ZC 6500). Sea of Japan: Oaji Beach, Koshino, Fukui Prefecture, 2 m, 22 May 2000, SCUBA, coll. T. Sugimoto, 1 male (sl 2.4 mm) (CBM-ZC 6501); Kaji, Mikuni, Fukui Prefecture, 2 m, 24 May 2001, SCUBA diving, coll. T. Sugimoto, 1 male (sl 3.0 mm) (CBM-ZC 6502); same locality, 28 Aug 2001, coll. T.

Sugimoto, 1 male (sl 1.7 mm) (CBM-ZC 6503); Saki, Mikuni, 2 m, 18 September 2001, SCUBA, coll. T. Sugimoto, 3 males (sl 1.5–1.6 mm), 1 female (sl 1.5 mm) (CBM-ZC 6504); Yasujima, Mikuni, 6 m, 27 Aug 2001, SCUBA diving, coll. T. Sugimoto, 2 females (sl 1.4, 2.8 mm) (CBM-ZC 6505); Takasa, Echizen, Fukui Prefecture, 2 m, 29 May 2001, SCUBA diving, coll. T. Sugimoto, 1 male (sl 2.9 mm) (CBM-ZC 6506).

Description. Eleven pairs of biserial phyllobranchiae.

Shield (Fig. 12A) 1.1-1.2 times as long as broad; rostrum triangular, well produced, terminating acutely, distinctly overreaching lateral projections, reaching anterior margin of interocular lobe, basally with tuft of short setae; lateral projections obtusely triangular, with or without small submarginal spine; anterior margin between rostrum and lateral projections concave; anterolateral margins sloping or slightly terraced; posterior margin roundly truncate; dorsal surface weakly convex, with some pairs of tufts of short setae laterally and 1 median tuft of setae; paragstric grooves inconspicuous. Posterior carapace generally membranous except for weakly calcified anterior part of posteromedian plate, with paired tufts of short to moderately long setae; cardiac sulci nearly subparallel, reaching beyond midlength of posterior carapace; sulci cardiobranchialis short.

Ocular peduncles (Fig. 12A) moderately slender, 0.6–0.7 of shield length, weakly inflated basally, with 2 rows of short setae on dorsomesial faces; corneas weakly dilated, maximal diameter subequal to basal diameter of peduncle. Ocular acicles (Fig. 12A) moderately separated basally, subovate, with submarginal terminal spine; dorsal surface slightly concave, with 1 or 2 short setae. Interocular lobe (Fig. 12A) with concave anterior surface.

Antennular peduncles (Fig. 12A), when fully extended, overreaching corneas by length of 0.1–0.2 of ultimate segment. Ultimate segment 1.4–1.6 times as long as penultimate segment, widened distally in lateral and ventral views. Basal segment unarmed on lateral face or laterodistal margin of statocyst lobe.



Fig. 12. *Pagurus erythrogrammus* sp. nov. A, shield and cephalic appendages, dorsal (setae on left antenna omitted); B, endopod of left maxillule, lateral; C, left third maxilliped, lateral; D, ischium and basis of left third maxilliped, dorsal (setae omitted); E, left fourth pereopod, lateral; F, coxae of fifth pereopods and eighth thoracic sternite, ventral; G, anterior lobe of sixth thoracic sternite, ventral; H, telson, dorsal. A, C-H, holotype male (sl 3.3 mm; CBM-ZC 6495); B, paratype male (sl 2.3 mm; CBM-ZC 6496).

Antennal peduncles (Fig. 12A) reaching or slightly overreaching corneas. Fifth and fourth segmens with few tufts of short setae. Third segment with small spine at ventromesial distal angle. Second segment with dorsolateral distal angle produced, reaching proximal 0.2-0.3 of fourth segment, terminating in simple or bifid spine, dorsomesial distal angle with small spine. First segment with spinule on lateral face distally, ventromesial distal margin produced, with small simple or bifid spine. Antennal acicle arcuate, reaching or overreaching base of cornea, terminating in sharp spine; mesial margin with row of rather sparse tufts of short to moderately long setae.

Mouthparts generally similar to those of *P. pilosipes.* External lobe of endopod of maxillule (Fig. 12B) recurved. Third maxilliped (Fig. 12C) moderately stout; propodus not widened; carpus unarmed on dorsodistal margin; merus unarmed on dorsodistal margin, but with spine on ventromesial margin; ischium (Fig. 12D) with well developed crista dentata and 1 accessory tooth; basis (Fig. 12D) with 2 small, but conspicuous teeth on mesial margin; exopod reaching midlength of carpus.

Right cheliped (Fig. 13A-C) larger than left cheliped. Chela subovate in dorsal view: fingers not strongly depressed dorsoventrally, without distinct hiatus. Dactylus slightly shorter than palm; dorsal surface with tufts of setae and single or double row of small spines on dorsal midline, dorsomesial margin delimited by row of small spines; mesial and ventral faces unarmed, but with row of tufts of setae; cutting edge with row of calcareous teeth of various size in proximal 0.7-0.8 and row of small corneous teeth in distal 0.2-0.3, terminating in small calcareous claw. Palm shorter than carpus; dorsal surface convex, with moderately spaced, small to moderately small spines arranged in 7 or 8 irregular rows (lateral rows extending onto fixed finger) usually obscured by dense covering of tufts of long plumose setae; dorsolateral and dorsomesial margins each delimited by row of small spines; lateral face with low, occasionally bifid protuberances and moderately short to long setae; mesial face with scattered, small, low tubercles, bifid or multifid,

low protuberances and tufts of setae; ventral surface with few low protuberances and scattered tufts of long setae. Cutting edge of fixed finger with row of calcareous teeth (1 subproximal tooth prominent), terminating in calcareous claw in males or corneous claw in females. Carpus subequal in length to merus, somewhat widened distally in dorsal view; dorsal surface with few tiny tubercles or spinules (occasionally with row of spinules on midline) and numerous tufts of long setae; dorsolateral margin not delimited; dorsomesial margin delimited by single or double row of small to moderately small spines; dorsodistal margin with row of tiny tubercles; lateral face dorsally with short denticulate ridges and tufts of long setae, ventrolateral margin with row of small spines distally; mesial face with low protuberances bearing long setae, ventromesial distal margin with small spines and tubercles; ventral surface somewhat inflated, with low protuberances and tufts of long setae. Merus with row of tufts of setae on dorsal surface and transverse ridges in distal half (distalmost ridge extending to mesial face), dorsodistal margin unarmed; lateral face with few tufts of setae dorsally and small tubercles ventrally, ventrolateral margin with row of small to moderately large spines and long setae; mesial face ventrally with small tubercles and low protuberances but otherwise smooth, ventromesial margin with row of small spines and long setae; ventral surface lacking prominent tubercle, with scattered tufts of long setae. Ischium with few tufts of setae on dorsal and ventral surfaces; ventromesial margin with row of obsolete tubercles.

Left cheliped (Fig. 14A-C) reaching base to midlength of dactylus of right cheliped. Chela subovate in dorsal view; no hiatus between fingers. Dactylus distinctly longer than palm, but not exceeding twice length of palm; dorsal surface with few tiny tubercles proximally and rows of tufts of short to moderately long setae, dorsomesial margin not delimited; mesial and ventral faces with tufts of moderately short to long setae; cutting edge with fine row of small corneous teeth. Palm distinctly shorter than carpus; dorsal surface somewhat elevated in midline, but not crested, with 2 irregular rows of moderReassessment of Pagurus pilosipes



Fig. 13. *Pagurus erythrogrammus* sp. nov. Right cheliped. A, chela and carpus, dorsal (setae omitted); B, entire cheliped, lateral; C, same, mesial (setae omitted). Holotype male (sl 3.3 mm; CBM-ZC 6495).

T. Komai



Fig. 14. *Pagurus erythrogrammus* sp. nov. Left cheliped. A, chela and carpus, dorsal (setae omitted); B, entire cheliped, mesial (setae omitted); C, same, lateral. Holotype male (sl 3.3 mm; CBM-ZC 6495).

ately small spines extending onto fixed finger and decreasing in size distally, mesial part with few small tubercles or spines; numerous tufts of long setae obscuring entire dorsal surface (including fixed finger); dorsolateral margin of palm proper not delimited but that margin of fixed finger weakly delimited by row of small spines; dorsomesial margin not delimited; lateral face with scattered low tubercles or protuberances and tufts of short setae; mesial face with few low tubercles and tufts of setae; ventral surface convex, with scattered tufts of long setae. Cutting edge of fixed finger with row of tiny calcareous teeth, 3 or 4 subdistal teeth interspersed with row of small corneous teeth. Carpus moderately compressed laterally, somewhat widened distally in dorsal view; dorsolateral and dorsomesial margins each with row of spines increasing in size distally and tufts of long setae, surface between margins unarmed; lateral face with scattered low tubercles and with tufts of short to moderately long setae, ventrolateral margin with row

of small spines; mesial face dorsally with large, low protuberances bearing long setae, ventrally with tufts of setae, ventromesial distal margin unarmed; ventral surface inflated, with small, low protuberances and tufts of long setae. Merus with row of short transverse ridges and moderately long setae on dorsal surface, dorsodistal margin unarmed; lateral face weakly granular, with moderately short setae dorsally, ventrolateral margin with row of moderately small spines; mesial face ventrally with large, low protuberances bearing long setae, but otherwise nearly smooth, ventromesial margin with row of small spines; ventral surface slightly concave, lacking prominent tubercle, but with scattered tufts of long setae. Ischium with row of small spines or tubercles on ventromesial margin.

Second pereopods (Fig. 15A) moderately long and slender; row of tufts of moderately short to long setae on dorsal and ventral surfaces of each segment. Dactyli 0.9-1.1 times as long as propodi, moderately slender (right dactylus at most 6.4 times as long as high); in lateral view nearly straight or slightly curved, in dorsal view, straight; terminating in large corneous claw; dorsal surfaces unarmed; lateral faces each with faint median sulcus and rows of tufts of long setae dorsally and ventrally; mesial faces (Fig. 15B) also faintly sulcate medially, with row of sparse setae dorsally, but unarmed or with 1 or 2 corneous spinules distally; ventral margins each with 7-11 long corneous spines. Propodi distinctly longer than carpi; dorsal surfaces unarmed; lateral and mesial faces each with rows of long setae dorsally and ventrally; ventral surfaces not tuberculate, with 4-6 corneous spines increasing in size distally on distal half. Carpi each with only dorsodistal spine on dorsal surface; lateral faces each with 2 rows of tufts of long setae on dorsal half. Meri each with low transverse ridges on dorsal surface; lateral faces each with few tufts of short setae; ventral margins each with row of small spines or low protuberances, ventrolateral distal margin usually smooth.

Third percopods (Fig. 15C, E) similar in males, dissimilar from right to left in females; setation generally similar to that of second pereopods. Dactyli 0.9-1.0 times as long as propodi (left dactylus at most 6.5 times as long as high); dorsal surfaces unarmed; lateral face only faintly sulcate, with rows of tufts of setae dorsally and ventrally (some ventral setae occasionally elongate and bearing numerous, long setules); mesial faces (Fig. 15D) each with row of 4-6 widely-spaced corneous spinules dorsally and 2 or 3 corneous spinules ventrally; ventral margins each with 7-12 long corneous spines. Propodi moderately slender; lateral face without ventral rows of small calcareous tubercles, but occasionally with some long plumose setae ventrally; ventral surface of left only slightly tuberculate in males (Fig. 15C), distinctly tuberculate in females, each with row of 5-7 long corneous spines (distalmost spine subequal or longer than distal spines on dactylus) (Fig. 15E). Carpi each with only dorsodistal spine on dorsal surface. Meri each with smooth ventral margin. Paired gonopores in females.

Fourth percopods (Fig. 12E) semichelate, generally similar to right to left; dorsal surfaces of propodi, carpi and meri and ventral surfaces of meri with numerous long setae. Dactylus nearly straight, terminating in small corneous claw, with row of small corneous teeth on ventral margin, lacking preungual process. Propodus moderately deep with convex ventral margin, rasp consisting of 3 or 4 rows of corneous scales; mesial face flat.

Fifth pereopod chelate; paired gonopores in males, left gonopore partially obscured by tufts of short setae (Fig. 12F).

Anterior lobe of sixth thoracic sternite (Fig. 12G) subsemicircular, slightly skewed to left, with numerous long setae on anterior surface. Eighth thoracic sternite (Fig. 12F) with 2 rounded lobes narrowly separated and slightly produced ventrolaterally, each with numerous setae anterolaterally.

Abdomen twisted. In males, 3 unpaired left pleopods; in females, 4 unpaired left pleopods.

Telson (Fig. 12H) with deep transverse indentations; posterior lobes with convex lateral margins bearing few long bristles; median cleft very small, occasionally indistinct; terminal margins weakly concave to somewhat oblique, each with 5–8 small spines.





Fig. 15. *Pagurus erythrogrammus* sp. nov. A, right second pereopod, lateral; B, dactylus of right second pereopod, mesial (only mesial setae illustrated); C, left third pereopod, lateral (setae omitted); D, dactylus of left third pereopod, mesial (only mesial setae illustrated); E, dactylus and propodus of left third pereopod. A-D, holotype male (sl 3.3 mm; CBM-ZC 6495); E, female paratype (sl 2.2 mm; CBM-ZC 6496).

Color in life (Fig. 25A). Shield gray, irregularly mottled with brown: posterior carapace olive grav spotted with white. Ocular peduncles light vellowish brown generally, with 2 reddish brown longitudinal stripes on dorsal surface at least distally. Antennular peduncles light brown, distal segment with 2 reddish brown longitudinal stripes on dorsal surface. Antennal peduncles also light brown generally; fifth segment with reddish brown longitudinal stripes on lateral and mesial faces. Right cheliped olive to brown, without longitudinal stripes on chela and carpus: dactvlus whitish: merus with irregular mottled pattern on dorsal, lateral and mesial surfaces, but distal part whitish. Coloration of left cheliped similar to that of right cheliped. Second and third pereopods (cf. Fig. 24C) with dactyli, propodi and carpi each striped by reddish brown on white background; lateral faces of dactyli each with 3 reddish brown stripes (including those on dorsal and ventral margins); distal part of propodi conspicuously white; lateral faces of propodi also each with 3 reddish brown stripes; dorsal surface of propodi white; lateral faces of carpi each with 3 reddish brown stripes; meri generally white, each with 2 reddish brown stripes on lateral face, dorsodistal part white, ventral margin sometimes reddish.

Size. Males: sl 1.5–4.0 mm; females sl 1.4–2.8 mm, ovigerous females 1.8–2.2 mm.

Distribution. Known from the Pacific coast of Japan from south of Boso Peninsula to Kii Peninsula; Sea of Japan from the coast of Fukui Prefecture; intertidal to 75 m. Found to use gastropod shells for microhabitat.

Variation. Setae on the right chela are usually extremely dense, obscuring the surface armature, but they are not very dense on the largest male specimen (CMNH-Cr 628). The density of the setae may be affected by secondary loss or damage of setae in large individuals.

The ventral surface of the propodus of the left third pereopod is more prominently tuberculate in females than in males.

Etymology. From the Greek *erythreus* (= red), and *grammus* (= lined), in reference to the reddish brown longitudinal stripes on the ambulatory legs.

Pagurus nigrivittatus sp. nov. (Figs. 16–19, 24D, 25B)

- Pagurus pilosipes—Miyake and Imafuku, 1980: 60, pl. 2, fig. 5; Miyake, 1982: 132, pl. 44, fig. 5; Oh, 1983: 101 (key), 106, pl. 1, figs. 3, 4, pls. 2, figs. 1–5; Takeda, 1986: 126, unnumbered fig.; Miyake, 1991: 132, pl. 44, fig. 5; Asakura, 1991: 798; Asakura, 1995: 363, pl. 97, fig. 9; Miyake, 1998: 132, pl. 44, fig. 5; Minemizu, 2000: 148, unnumbered fig. Not Pagurus pilosipes Stimpson, 1858.
- Pagurus dubius—Matsukubo, 1999: 170, unnumbered fig., 284. Not Pagurus dubius (Ortmann, 1892).

Material examined. Holotype. Sabiura Beach, Kushimoto, Kii Peninsula, 7 m, 10 May 1995, SCUBA diving, coll. K. Nomura, male (sl 3.6 mm) (CBM-ZC 6481).

Paratypes. Japan. Boso Peninsula: Hasama Beach, Tateyama, 34° 58.4N, 139° 47.5E, intertidal, 5 May 1996, hand, coll. T. Komai, 2 males (sl 1.7, 2.7 mm), 2 females (sl 1.9, 2.8 mm) (CBM-ZC 6482); similar locality, 16 May 1996, hand, coll. T. Komai, 2 males (sl 2.1, 2.8 mm), 1 ovigerous (sl 2.2 mm) (CBM-ZC 6483); Sunosaki Fishing Port, Tatevama, 3 m, 16 January 1997, trap, coll. T. Komai, 1 male (sl 2.2 mm) (CBM-ZC 6484); Tatsushima Fishing Port, Katsuyama, 35°05.5N, 139°49.8E, 2-3 m, July 1997, trap, coll. T. Komai, 1 male (sl 3.4 mm) (CBM-ZC 6485); Hota Fishing Port, Kyonan, 3 m, 2 February 2000, trap, coll. T. Komai, 1 female (sl 3.5 mm) (CBM-ZC 6486). Sagami Bay: Futo, Izu Peninsula, 0-5 m, 1995, SCUBA diving, coll. M. Mitsuhashi, 2 males (sl 1.9, 3.0 mm), 5 females (sl 1.9-2.7 mm) (CBM-ZC 6487). Izu Islands: Sokodo, Hachijo-jima Island, 5 m, 12 September 2001, SCUBA diving, coll. J. Okuno, 1 female (sl 3.4 mm) (CMNH-ZC 1008); same data, 1 female (sl 4.0 mm) (CMNH-ZC 1009). Kii Peninsula: Sabiura, Kushimoto, 5 m, January 1992, SCUBA, coll. K. Nomura, 2 males (sl 2.5, 3.5 mm), 1 ovigerous (sl 2.6 mm) (MNHN-Pg 6342); Sabiura Beach, Kushimoto, intertidal, 3 February 1995, hand, coll. T. Komai, 3 males (sl 1.8-3.3 mm), 1 female (sl 1.9 mm), 1 ovigerous female (sl 2.1 mm) (USNM 1010244); Kamiura Beach, Kushimoto, intertidal, 3 February 1995, hand, coll. T. Komai, 1 male (sl 3.6 mm) (CBM-ZC 6489); Rinkai, Shirahama, intertidal, 19 October 1976, hand, coll. M. Imafuku, 2 males (sl 2.3, 2.4 mm) (OMNH-Ar 1792-1793); same locality, 27 May 1976, hand, coll. M. Imafuku, 1 male (sl 3.3 mm) (OMNH-Ar 1897); same locality, 22 October 1975, coll. M. Imafuku, 2 males (3.1, 3.3 mm) (OMNH-Ar 1901–1902). Tosa Bay: Shirigai, Ohtsuki, intertidal, 9 September 1995, hand, coll. K. Nomura, 2 males (sl 2.7, 2.9 mm) (CBM-ZC 6490). Kyushu: Shifushi, Kagoshima Prefecture, 5 m, 31 March 1997, gill net, coll. T. Kurozumi, 1 male (sl 4.1 mm) (CBM-ZC 3611). Sea of Japan: Kaji, Mikuni, Fukui Prefecture, intertidal, 24 May 2001, hand, coll. T. Sugimoto, 1 male (sl 2.7 mm) (CBM-ZC 6491); Takasa, Echizen, Fukui Prefecture, 2 m, 29 May 2001, SCUBA diving, coll. T. Sugimoto, 1 female (sl 1.8 mm) (CBM-ZC 6488); same locality, intertidal, 25 September 2001, hand, coll. T. Sugimoto, 3 males (sl 2.3-3.2 mm), 3 ovigerous females (sl 2.2-2.3 mm) (CBM-ZC 6621); Sou, Echizen, Fukui Prefecture, intertidal, 3 September 2001, hand, coll. T. Sugimoto, 5 males (sl 2.0-2.6 mm) (CBM-ZC 6492); similar locality, 2 m, SCUBA diving, coll. T. Sugimoto, 3 males (sl 1.5-2.9 mm), 1 ovigerous female (sl 1.8 mm) (CBM-ZC 6493).

Taiwan. Taipei County: Ma Kun Beach, intertidal, 3 August 1996, hand, coll. T. Komai, 3 males (sl 2.6–3.4 mm), 2 females (sl 1.5, 1.5 mm) (CBM-ZC 6494); 2 males (sl 2.6, 2.6 mm), 2 females (sl 1.9, 2.5 mm) (NTOU P-1996-8-5).

Description. Eleven pairs of biserial phyllobranchiae.

Shield (Fig. 16A) 1.0-1.1 times as long as wide; rostrum triangular or rounded, terminating bluntly to acutely, overreaching lateral projections, occasionally reaching anterior margin of interocular lobe, with a pair of tufts of setae basally; lateral projections obtusely triangular, each with submarginal spinule; anterior margin between rostrum and lateral projections concave; anterolateral margins sloping; posterior margin roundly truncate; dorsal surface slightly convex, with some pairs of tufts of short to moderately long setae laterally and 1 or 2 median tufts of setae; paragastric grooves inconspicuous. Posterior carapace similar to that of P. insulae.

Ocular peduncles (Fig. 16A) moderately slender, 0.6–0.7 times as long as shield, weakly inflated basally, with row of tufts of long setae dorsomesially; corneas slightly dilated, maximal diameter subequal to basal diameter of ocular peduncle. Ocular acicles (Fig. 16A) subovate, moderately separated basally, with small submarginal spine; dorsal surface slightly concave, with few setae. Interocular lobe small, visible in dorsal view, with slightly concave anterior surface.

Antennular peduncles (Fig. 16A) reaching or slightly overreaching corneas. Ultimate segment 1.4–1.5 times as long as penultimate segment, somewhat widened distally in lateral view, with few short setae on dorsal surface. Basal segment unarmed on lateral face or laterodistal margin of statocyst lobe.

Antennal peduncles (Fig. 16A) not reaching or reaching corneas. Fifth and fourth segments with few short setae. Third segment with small spine at ventromesial distal angle. Second segment with dorsolateral distal angle produced, reaching proximal 0.3-0.5 of fourth segment, terminating in simple or bifid spine, dorsomesial distal angle with small spine. First segment unarmed or with spinule on lateral face distally, ventromesial distal margin with 1 or 2 spinules laterad of antennal gland opening Antennal acicle arcuate, reaching beyond base of cornea, but not reaching distal margin of cornea, terminating in sharp spine, with numerous setae on mesial margin. Antennal flagellum long, distinctly overreaching fully extended right cheliped; articles each with minute setae on distal margins.

Mouthparts generally similar to those of *P. insulae*; endopod of maxillule (Fig. 16B) with weakly produced inner lobe, outer lobe obsolete. Third maxilliped (Fig. 16C) moderately stout; propodus not widened; carpus unarmed on dorsodistal margin; merus unarmed on dorsodistal or ventromesial margins; ischium with well-developed crista dentata and 1 accessory tooth (Fig. 16D); basis with 1 or 2 small teeth on mesial margin (Fig. 16D); exopod reaching or slightly overreaching distal margin of merus.

Right cheliped (Figs. 17A-D, 18A, B) larger than left cheliped, but not greatly elongate even in large males. Chela subovate in dorsal



Fig. 16. *Pagurus nigrivittatus* sp. nov. A, shield and cephalic appendages, dorsal (setae on left antenna omitted); B, endopod of left maxillule, lateral; C, left third maxilliped, lateral; D, ischium and basis of left third maxilliped, dorsal; E, left fourth pereopod, lateral; F, coxae of fifth pereopods and eighth thoracic sternite, ventral; G, anterior lobe of sixth thoracic sternite; H, telson, dorsal. Holotype male (sl 3.6 mm; CBM-ZC 6481).



Fig. 17. *Pagurus nigrivittatus* sp. nov. Right cheliped. A, chela, dorsal (setae omitted); B, carpus, dorsal (setae omitted); C, entire cheliped, lateral; D, same mesial (setae omitted). Holotype male (sl 3.6 mm; CBM-ZC 6481).

view, 1.7-1.8 times as long as greatest width at level of midlength of palm; fingers not particularly depressed dorsoventrally; narrow hiatus between fingers in males, no hiatus in females. Dactylus slightly shorter to slightly longer than palm; dorsal surface with median and dorsomesial rows of small spines and occasionally with several additional spines mesiad of median row, and with tufts of moderately short setae; mesial and ventral faces with few small tubercles or low protuberances and tufts of short setae; cutting edge in males with row of small calcareous teeth, terminating in calcareous or small corneous claw; cutting edge in females with row of larger calcareous teeth in proximal 0.5-0.6 and row of small corneous teeth in distal 0.4-0.5, terminating corneous claw. Palm distinctly shorter than carpus; dorsal surface convex, sloping to mesial face without delineation of dorsomesial margin, with numerous, but not very dense, small to moderately small, scattered spines extending onto fixed finger (males) or with moderately small spines arranged in 6-8 irregular rows (females), and with tufts of moderately short to long setae; dorsolateral margin delimited by row of small spines increasing in size on fixed finger; lateral face with scattered, low, rounded tubercles and short to moderately long setae; mesial face with small spinulose or low tubercles and moderately long setae; ventral surface weakly convex, with scattered low tubercles or protuberances and tufts of long setae. Cutting edge of fixed finger with low calcareous teeth, terminating in calcareous claw in males; bearing row of small calcareous teeth in proximal 0.6 and row of small corneous teeth in distal 0.4, terminating in corneous claw in females. Carpus moderately short to moderately long (at most 1.5 times longer than distal width), subequal in length to merus; dorsal surface sloping to lateral face, with scattered tiny tubercles laterally and irregular single row of small spines on midline, and scattered tufts of moderately long setae; dorsomesial margin delimited by single or double row of small to moderately small spines; lateral face with small, low tubercles or protuberances and moderately short to long setae; mesial face with low, occasionally bifid tubercles or protuberances and moderately short to long setae: ventral surface moderately inflated, with scattered small tubercles or protuberances, and long setae. Merus with row of short transverse ridges and moderately short to long setae on dorsal surface, distalmost ridge denticulate, extending onto lateral and mesial faces: dorsodistal margin unarmed; lateral face with few tufts of short setae dorsally and few small tubercles ventrally, ventrolateral margin with row of small spines (margin more sharply delimited in females than in males); mesial face with few tufts of setae dorsally and small tubercles ventrally, ventromesial margin not distinctly delimited: ventral surface weakly convex, with scattered small spines and long setae, and frequently with 1 prominent tubercle. Ischium with short to moderately short setae on every surface; ventromesial margin with row of spinules; ventrolateral margin unarmed.

Left cheliped (Fig. 18C-F) reaching midlength of palm of right chela to midlength of dactylus of right cheliped. Chela subovate in dorsal view, 1.9-2.2 times as long as wide; prominent hiatus between fingers in males. Dactylus exceeding twice length of palm; dorsal surface with some tiny spines proximally and tufts of short to moderately long setae, dorsomesial margin not delimited; mesial face unarmed, but with tufts of long setae; ventral surface with tufts of long setae; cutting edge with row of small corneous teeth. Palm about half length of carpus; dorsal surface somewhat elevated in midline, but not crested, with 2 median rows of moderately small to large spines extending onto fixed finger; lateral part of dorsal surface with scattered small spines or tubercles extending onto fixed finger, ventrolateral margin not delimited (in males) or rather distinctly delimited by row of small spines or tubercles (in females); mesial part of dorsal surface with short row of small spines or tubercles; mesial face with few short, occasionally denticulate ridges dorsally and long setae; ventral surface slightly convex, with few tufts of long setae. Cutting edge of fixed finger with row of small corneous teeth. Carpus somewhat compressed laterally, slightly widened distally in dorsal view; dor-



Fig. 18. Pagurus nigrivittatus sp. nov. Chelipeds, setae omitted. A, right chela, dorsal; B, merus of right cheliped, lateral; C, left chela, lateral; D, chela and carpus of left cheliped, dorsal; E, left cheliped, lateral; F, same, mesial. A-C, paratype female (sl 3.5 mm; CBM-ZC 6486); D-F, holotype male (sl 3.6 mm; CBM-ZC 6481).

solateral and dorsomesial margins each delimited by row of moderately large spines and tufts of long setae, dorsal surface unarmed; lateral face with scattered low, occasionally bifid tubercles, and short to long setae, ventrolateral margin with row of small spines; mesial face with large, low protuberances accompanied by tufts of long setae;



Fig. 19. *Pagurus nigrivittatus* sp. nov. A, right second pereopod, lateral; B, dactylus of right second pereopod, mesial (only mesial setae illustrated); C, left third pereopod, lateral (setae omitted); D, dactylus of left third pereopod, mesial (only mesial setae illustrated); E, dactylus and propodus of left third pereopod, lateral. A-D, holotype male (sl 3.6 mm; CBM-ZC 6481); E, paratype female (sl 3.5 mm; CBM-ZC 6486)

ventral surface weakly inflated, with small tubercles and tufts of long setae. Merus with row of short transverse ridges and moderately short to long setae on dorsal surface, dorsodistal margin unarmed; lateral face with tiny, low tubercles and few short setae, ventrolateral margin with 5-7 moderately small spines; mesial face almost smooth, with tufts of long setae ventrally, ventromesial margin with row of small spines; ventral surface slightly convex, with scattered small spines or tubercles and tufts of long setae, and usually with 1 prominent tubercle (sometimes reduced in males). Ischium with row of small spines on ventromesial margin; tufts of long setae on lateral and ventral surfaces.

Second percopods (Fig. 19A) moderately long and slender; row of tufts of moderately short to long setae on dorsal and ventral surfaces of each segment (except for coxae). Dactyli 0.8–1.0 times as long as propodi, moderately slender (right dactylus at most 6.2 times as long as high); in lateral view weakly curved, in dorsal view, straight; terminating in large corneous claw; dorsal surfaces unarmed; lateral faces each with shallow median sulcus and rows of tufts of long setae dorsally and ventrally; mesial faces each with row of tufts of long setae ventrally, unarmed or occasionally with 1 spinule dorsally near base of claw (Fig. 23B); ventral margins each with 5-7 short corneous spines. Propodi moderately short to long, distinctly longer than carpi; dorsal surfaces unarmed; lateral and mesial faces each with rows of tufts of long setae dorsally and ventrally; ventral surfaces not tuberculate, with 3 or 4 widely-spaced, short corneous spines in distal half. Carpi each with only dorsodistal spine on dorsal surface; lateral faces each with 2 rows of tufts of long setae on dorsal half. Meri each with low transverse ridges on dorsal surface; lateral faces each with few tufts of setae distally; ventral margins each with row of small spines or low protuberances, ventrolateral distal margins with some spinules.

Third percopods (Fig. 15C, E) dissimilar from right to left; setation generally similar to that of second percopods. Dactyli 1.0–1.1 times as long as propodi; dorsal surfaces unarmed; lateral face smooth in both males and

females (right) or with short rows of small calcareous tubercles ventrally (left; occasionally reduced in males); mesial faces each with row of 3-5 widely-spaced corneous spinules adjacent to dorsal margin and 1 or 2 corneous spinules on midline (Fig. 23D); ventral margins each with 5-7 short corneous spines. Propodi moderately slender in males, stout in females, lateral face smooth (right) or bearing ventrolateral rows of small calcareous tubercles (left; occasionally reduced in large males); ventral surface of left slightly to somewhat tuberculate, terminating distally in small spine, with row of 3 or 4 short corneous spines mesially (distalmost spine shorter than distal spines on dactylus). Carpi each with only dorsodistal spine on dorsal surface. Meri each with smooth ventral margin. Paired gonopores in females.

Fourth percopods (Fig. 12E) semichelate, generally similar to right to left; dorsal surfaces of propodi, carpi and meri and ventral surfaces of meri with numerous long setae. Dactylus straight or slightly curved, terminating in small corneous claw, with row of small corneous teeth on ventral margin; preungual process absent. Propodus moderately deep with convex ventral margin, rasp consisting of 4 or 5 rows of corneous scales; mesial face flat.

Fifth pereopods chelate; paired gonopores in males, left gonopore partially obscured by tufts of short setae (Fig. 12F).

Anterior lobe of sixth thoracic sternite (Fig. 12G) subsemicircular, slightly skewed to left, with numerous long setae on anterior surface. Eighth thoracic sternite (Fig. 12F) with 2 rounded lobes narrowly separated and slightly produced ventrolaterally, each with numerous setae anterolaterally.

Abdomen twisted. In males, 3 unpaired left pleopods; in females, 4 unpaired left pleopods.

Telson (Fig. 12H) with deep transverse indentations; posterior lobes with convex lateral margins bearing few long bristles; median cleft small; terminal margins somewhat oblique, with 4 or 5 large calcareous spines and occasionally with few interspersed spinules.

Coloration in life (Fig. 25C). Shield light gray, with faint dark brown markings laterally. Right cheliped generally dark gray-

brown; distal part of dactylus whitish; spines on dorsal surface and low protuberances on ventral surface paler; carpus with white longitudinal stripe on dorsal surface mesially; spines comprising dorsomesial rows of carpus dark gray-brown, while spines on dorsal surface whitish; darker, irregularly spotted markings on lateral and mesial faces of carpus; merus with white transverse band subdistally, dark gray-brown area on lateral and mesial faces irregularly spotted by white. Color pattern of left cheliped generally similar to that of right, but marking on mesial face of carpus forming clear median stripe. Ambulatory legs (cf. Fig. 24D) generally white with distinct dark gray-brown stripes; dactyli with dorsal and ventral surfaces dark gray-brown, lateral and mesial faces each with median stripe; propodi and carpi with white dorsal and dark gray-brown ventral surfaces, lateral and mesial faces each with 2 distinct stripes (one dorsal and one median); dorsal stripes on propodi not reaching distal end; meri each with 3 slightly oblique stripes on lateral face.

Size. Male sl 1.7-4.1 mm; females sl 1.9-3.5 mm, ovigerous females sl 1.8-2.1 mm.

Variation. The shape of the rostrum varies from rounded to triangular.

The spines on the dorsal surface of the right palm are smaller and more numerous in males than in females.

The variation in the development of the ventral tubercle on the cheliped meri may be different between males and females. The ventral tubercle on the merus of the right cheliped is absent or rudimentary in 13 of 30 males (43.3%), but while in females, it is poorly developed in only three of 17 individuals (17.6%). The ventral tubercle on the left cheliped is poorly developed in six of 30 males (20.0%); it is well developed in all females examined.

The ventrolateral tubercles on the dactylus and propodus of the left third pereopod are well developed in females and small males, but they tend to be reduced in large males (sl 3.1-4.1 mm).

Distribution. Known from the Pacific coast of Japan from Boso Peninsula southward to Kyushu; Mikuni, Fukui Prefecture, Sea of Japan; northeast of Taiwan; intertidal to 7 m. Found to use gastropod shells for microhabitat.

Etymology. From the Latin *niger* (=black), and *vittatus* (=ornamented with ribbon), in reference to the dark brown longitudinal stripes on the ambulatory legs.

Pagurus quinquelineatus sp. nov. (Figs. 20–23, 24B, 25A)

Pagurus pilosipes—Miyake, 1978: 91 (part), fig. 34d. Not Pagurus pilosipes (Stimpson, 1858). See "Discussion."

Material examined. Holotype. Suruga Bay: Heda Fishing Port, Izu Peninsula, 3 m, 20 March 2001, trap, coll. T. Komai, male (sl 4.0 mm) (CBM-ZC 6593).

Paratypes. Boso Peninsula: Hota Fishing Port, Kyonan, intertidal, 14 February 1997, hand, coll. T. Komai, 1 ovigerous female (sl 4.2 mm) (CBM-ZC 6592); Katsuyama Fishing Port, Kyonan, 2-3 m, 20 September 2002, trap, coll. T. Komai, 2 males (sl 3.1, 3.6 mm) (CBM-ZC 6622). Sagami Bay: Kamegi-sho, 14 m, 24 July 1960, dredge, 1 male (sl 3.0 mm), Miyake (1978) det. no. 387 (NSMT-CrR 1805); same locality, 14 m, 25 July 1960, dredge, 1 female (sl 2.8 mm), Miyake (1978) det. no. 395 (NSMT-CrR 1813); same locality, 16 m, 28 July 1960, dredge, 1 male (sl 2.3 mm), Miyake (1978) det. no. 410 (NSMT-CrR 1828); same locality, 12-14 m, 14 July 1962, dredge, 1 ovigerous female (sl 4.6 mm), Miyake (1978) det. no. 471 (NSMT-CrR 2020); same locality, 16 m, 25 July 1964, dredge, 1 male (sl 3.2 mm), 1 female (sl 2.7 mm), Miyake det. no. 559 (NSMT-CrR 2254). Suruga Bay: same data as holotype, 1 ovigerous female (sl 3.4 mm) (CBM-ZC 6594). Sea of Japan: Sou, Echizen, Fukui Prefecture, 2m, 28 May 2001, SCUBA, coll. T. Sugimoto, 1 male (sl 2.6 mm) (CBM-ZC 6589); similar locality, 10 m, 28 May 2001, SCUBA, coll. T. Sugimoto, 1 female (sl 3.2 mm) (CBM-ZC 6590); similar locality, 6 m, 3 September 2001, SCUBA, coll. T. Sugimoto, 1 male (sl 1.7 mm) (CBM-ZC 6591).

Description. Eleven pairs of biserial phyllobranchiae.

Shield (Fig. 20A) 1.0–1.1 times as long as broad; rostrum broadly triangular, terminating bluntly, overreaching lateral projections,

T. Komai



Fig. 20. *Pagurus quinquelineatus* sp. nov. A, shield and cephalic appendages, dorsal (setae on left side omitted); B, endopod of left maxillule, lateral; C, left third maxilliped, lateral; D, ischium and basis of left third maxilliped, dorsal (setae omitted); E, left fourth pereopod, lateral; F, coxae of fifth pereopods and eighth thoracic sternite, ventral; G, anterior lobe of sixth thoracic sternite, ventral; H, telson, dorsal. Holotype male (sl 4.0 mm; CBM-ZC 6593).

but not reaching anterior margin of interocular lobe, basally with pair of tufts of long setae; lateral projections obtuse, with or without small submarginal spine; anterior margin between rostrum and lateral projections slightly concave; anterolateral margins sloping; posterior margin roundly truncate; dorsal surface weakly convex, with several pairs of tufts of short to long setae laterally and 1 median tuft of setae; paragstric grooves inconspicuous. Posterior carapace generally membranous except for weakly calcified anterior part of posteromedian plate, with paired tufts of short to moderately long setae; cardiac sulci nearly subparallel, reaching beyond midlength of posterior carapace; sulci cardiobranchialis short.

Ocular peduncles (Fig. 20A) relatively slender, 0.6–0.8 of shield length, slightly inflated basally, with 2 rows of short setae on dorsomesial faces; corneas not dilated, maximal diameter subequal to basal diameter of peduncle. Ocular acicles (Fig. 20A) moderately separated basally, subovate, each with submarginal terminal spine; dorsal surface slightly concave, with 1 or 2 setae. Interocular lobe (Fig. 20A) with concave anterior surface.

Antennular peduncles (Fig. 20A), when fully extended, overreaching corneas by length of 0.1–0.2 of ultimate segment. Ultimate segment 1.3–1.4 times as long as penultimate segment, widened distally in lateral and ventral views. Basal segment unarmed on lateral face or laterodistal margin of statocyst lobe.

Antennal peduncles (Fig. 20A) not reaching to slightly overreaching corneas. Fifth and fourth segmens with few tufts of short setae. Third segment with small spine at ventromesial distal angle. Second segment with distolateral distal angle produced, reaching proximal 0.2-0.3 of fourth segment, terminating in simple or bifid spine, dorsomesial distal angle with small spine. First segment with spinule on lateral face distally, ventromesial distal margin produced, with minute spine just lateral of antennal Antennal acicle arcuate, gland opening. reaching or overreaching base of cornea, but not reaching distal margin of cornea, terminating in sharp spine; mesial margin with row of tufts of short to moderately long setae. Antennal flagellum far overreaching tip of extended right cheliped.

Mouthparts generally similar to those of *P. pilosipes.* External lobe of endopod of maxillule (Fig. 20B) recurved. Third maxilliped (Fig. 20C) moderately slender; propodus not widened; carpus unarmed on dorsodistal margin; merus unarmed on dorsodistal spine, but with spine on ventromesial margin; ischium (Fig. 20D) with well developed crista dentata and 1 accessory tooth; basis (Fig. 20D) with 2 small, but conspicuous teeth on mesial margin; exopod reaching midlength of carpus.

Right cheliped (Fig. 21A-D) larger than left cheliped. Chela subtriangular in dorsal view; fingers not strongly depressed dorsoventrally; no distinct hiatus between fingers. Dactylus slightly shorter than palm; dorsal surface with tufts of setae and single row of small spines on dorsal midline, dorsomesial margin delimited by row of small spines; mesial face occasionally with few small spines proximally; ventral surface unarmed, but with row of tufts of long setae; cutting edge with row of calcareous teeth of various size in proximal 0.7-0.8 and row of small corneous teeth in distal 0.2-0.3, terminating in small calcareous claw. Palm shorter than carpus; dorsal surface convex, with moderately-spaced small to moderately small spines arranged in 6 or 7 irregular rows (lateral rows extending onto fixed finger) and numerous tufts of long setae; dorsolateral and dorsomesial margins each delimited by row of moderately small spines; lateral face with small, low protuberances and tufts of moderately short to long setae; mesial face with scattered, low protuberances and tufts of long setae; ventral surface with scattered tufts of long setae. Cutting edge of fixed finger with row of calcareous teeth of various sizes, terminating in small calcareous claw (males) or corneous claw (females). Carpus slightly shorter than merus, somewhat widened distally in dorsal view; dorsal surface with small spines or tubercles and numerous tufts of long setae, dorsolateral margin obscure but with row of small spines; dorsomesial margin delimited by single or double row of large spines; dorsodistal margin with few small spines; lateral face dorsally with some





Fig. 21. *Pagurus quinquelineatus* sp. nov. Right cheliped. A, chela, dorsal (setae omitted); B, carpus, dorsal (setae omitted); C, entire cheliped, lateral; D, same, mesial (setae omitted). Holotype male (sl 4.0 mm; CBM-ZC 6593).

short, denticulate ridges and tufts of long setae, ventrolateral margin with row of small spines distally; mesial face with low protuberances bearing long setae, ventromesial margin almost smooth; ventral surface somewhat inflated, with low protuberances and tufts of long setae. Merus with row of tufts of setae and short transverse ridges on dorsal surface (distalmost ridge occasionally extending onto mesial face), unarmed on dorsodistal margin; lateral face with few tufts of long setae, ventrolateral margin with row of small to moderately small spines and long setae; mesial face with few short ridges, ventromesial margin with row of spines increasing in size proximally and long setae; ventral surface only slightly convex proximally, without prominent tubercle, but with scattered tufts of long setae. Ischium with few tufts of setae on dorsal and ventral surfaces; ventromesial margin with row of obsolete tubercles.

Left cheliped (Fig. 22A-C) slightly overreaching base of dactylus of right cheliped in males, reaching beyond midlength of dactylus in females. Chela subovate in dorsal view; no hiatus between fingers. Dactylus distinctly longer than palm, but not exceeding twice length of palm; dorsal surface with rows of tufts of short to moderately long



Fig. 22. *Pagurus quinquelineatus* sp. nov. Left cheliped. A, chela and carpus, dorsal (setae omitted); B, entire cheliped, lateral; C, same, mesial (setae omitted). Holotype male (sl 4.0 mm; CBM-ZC 6593).

setae and occasionally with few tiny tubercles proximally, dorsomesial margin not delimited; mesial and ventral faces with tufts of moderately short to long setae; cutting edge with fine row of small corneous teeth in distal 0.5–0.6. Palm distinctly shorter than carpus; dorsal surface weakly elevated in midline, with 2 rows of moderately small spines extending onto fixed finger and decreasing in size distally, mesial part with few small tubercles or spines; numerous tufts of long setae present on dorsal surface including fixed finger; dorsolateral margin of palm weakly delimited by row of spines extending at least to midlength of fixed finger; dorsomesial margin not delimited; lateral face with few small tubercles or protuberances and tufts of short to long setae; mesial face also with few small tubercles and tufts of setae; ventral surface convex, with scattered tufts of long setae. Cutting edge of fixed finger with row of tiny calcareous teeth, subdistal teeth interspersed with row of small corneous teeth. Carpus moderately compressed laterally, somewhat widened distally in dorsal view; dorsolateral and dorsomesial margins each with row of moderately large spines increasing in size distally and tufts of long setae, dorsal surface between margins unarmed; lateral face with scattered low protuberances and tufts of long setae, ventrolateral margin slightly tuberculate; mesial face dorsally with low ridges accompanied by setae and ventrally with tufts of setae, ventromesial distal margin smooth; ventral surface inflated, with tufts of long setae. Merus with row of short transverse and moderately long setae on dorsal surface, dorsodistal margin unarmed; lateral face smooth, with moderately short setae dorsally, ventrolateral margin with row of moderately large spines; mesial face ventrally with low protuberances accompanied by long setae, but otherwise almost smooth, ventromesial margin with row of small spines; ventral surface slightly concave, lacking prominent tubercle, but with scattered tufts of long setae. Ischium with row of small spines or tubercles on ventromesial margin.

Second percopods (Fig. 23A) relatively long and slender; row of tufts of moderately short to long setae on dorsal and ventral surfaces of each segment. Dactyli 0.9-1.1 times as long as propodi, at most 7.2 times as long as high; in lateral view slightly curved, in dorsal view straight; terminating in large corneous claw; dorsal surfaces unarmed; lateral faces not sulcate medially, but with row of tufts of long setae dorsally and ventrally; mesial faces not sulcate medially, with row of corneous spinules and sparse setae dorsally (Fig. 23B); ventral margins each with 8-14 long corneous spines. Propodi relatively slender, distinctly longer than carpi; dorsal surfaces unarmed; lateral and mesial faces each with rows of long setae dorsally and ventrally; ventral surfaces not tuberculate, with 4-6 long corneous spines in distal half. Carpi each with only dorsodistal spine on dorsal surface; lateral faces each with 2 rows of tufts of long setae on dorsal half. Meri with low transverse ridges on dorsal surfaces; lateral faces each with few tufts of short setae; ventral margins each with row of small spines or low protuberances, ventrolateral distal margin usually unarmed.

Third pereopods (Fig. 23C) generally similar from right to left; setation generally similar to that of second pereopods. Dactyli 1.1-1.2 times as long as propodi; dorsal surfaces unarmed; lateral faces lacking calcareous tubercles in both males and females, not sulcate medially, with rows of tufts of setae dorsally and ventrally; mesial faces each with row of widely-spaced corneous spinules adjacent to dorsal margin and 2-4 corneous spinules adjacent to ventral margin (Fig. 23D); ventral margins each with 9-15 long corneous spines. Propodi without ventral rows of small calcareous tubercles on lateral faces; ventral surface of left nearly straight in males (Fig. 23D), weakly concave in females (Fig. 23E), with row of 5-7 corneous spines increasing in size distally (distalmost spine subequal to or longer than distal spines on dactylus). Carpi each with only dorsodistal spine on dorsal surface. Meri each with smooth ventral margin. Paired gonopores in females.

Fourth percopods (Fig. 16E) semichelate, generally similar to right to left; dorsal surfaces of propodi, carpi and meri and ventral surfaces of meri with numerous long setae. Dactylus nearly straight, terminating in Reassessment of Pagurus pilosipes



Fig. 23. *Pagurus quinquelineatus* sp. nov. A, right second pereopod, lateral; B, dactylus of right second pereopod, mesial (only mesial setae illustrated); C, left third pereopod, lateral (setae mostly omitted); D, dactylus of left third pereopod (only mesial setae illustrated); E, dactylus and propodus of left third pereopod, lateral (setae omitted). A–D, holotype male (sl 4.0 mm; CBM-ZC 6593); E, paratype female (sl 3.4 mm; CBM-ZC 6594).

small corneous claw, with row of small corneous teeth on ventral margin, lacking preungual process. Propodus moderately deep with convex ventral margin, rasp consisting of 3 or 4 rows of corneous scales; mesial face flat.

Fifth percopods chelate; paired gonopores in males, left gonopore partially obscured by tufts of short setae (Fig. 16F).

Anterior lobe of sixth thoracic sternite (Fig. 16G) subsemicircular, with numerous long setae on anterior surface. Eighth thoracic sternite (Fig. 16F) with 2 rounded lobes narrowly separated and slightly produced ventrolaterally, each with numerous setae anterolaterally.

Abdomen twisted. In males, 3 unpaired left pleopods; in females, 4 unpaired left pleopods.

Telson (Fig. 16H) with deep transverse indentations; posterior lobes with convex lateral margins bearing few long bristles; median cleft wide; terminal margins slightly oblique, each with 5–7 small corneous-tipped spines.

Color in life (Fig. 25A). Shield mottled with light yellow brown and dark olive, occasionally with irregular mottled pattern of brick red; posterior carapace bluish gray spotted with white. Ocular peduncles pale brown generally, with broad dark brown longitudinal stripe on mesial face. Antennular peduncles light brown, distal segment with 2 brown or brick red longitudinal stripes on dorsal surface. Antennal peduncles also light brown generally; fifth segment with brown or brick red longitudinal stripes on lateral and mesial faces. Right cheliped generally olive; dactylus with 2 brown or brick red stripes on dorsal surface and mesial face, respectively; palm with 2 rather obsolete brick red stripes on dorsal surface and with irregularly mottled pattern of brown; carpus with 2 broad brown stripes on dorsal surface, lateral and mesial faces each with large brick red blotch; merus mottled by brick red. Coloration of left cheliped generally similar to that of right cheliped; dactylus with 2 brick red stripes dorsally and 1 stripe mesially; chela with 3 stripes on dorsal surface (but occasionally obsolete); carpus with 2 narrow stripes on dorsal surface and 1 very broad stripe on mesial face, lateral face with large blotch. Second and third percopods (cf. Fig. 24B) striped by brown or brick red on pale yellowish brown background; 5 stripes visible on lateral faces of dactyli (including stripes on dorsal and ventral surfaces and 3 stripes on lateral faces proper); similarly 5 stripes visible on lateral faces of propodi; carpi each with 1 stripe on dorsal surface and 4 or 5 stripes on lateral face (ventralmost stripe occasionally obscure or absent); meri each with 4 stripes on lateral face (dorsalmost one sinuously curved).

Size. Males sl 1.7–4.0 mm; females sl 2.7–4.6 mm, ovigerous females 3.4–4.6 mm.

Distribution. Pacific coast of Japan from Boso Peninsula, Sagami Bay and Suruga Bay; Sea of Japan coast from Mikuni, Fukui Prefecture; intertidal to 16 m. Found to use gastropod shells for microhabitat.

Etymology. From the Latin *quinque* (=five), and *lineatus* (=lined), and referring to the characteristic five longitudinal stripes visible on the lateral faces of the propodi of the ambulatory legs.

Comparison

Five species treated in this study are generally similar to one another. They are distinguished from all other western and northern Pacific species of *Pagurus* by a set of the following characters: the palm of the right cheliped is spinose; the propodus of the right second pereopod is unarmed on the dorsal surface; the carpus of the right second pereopod is armed only with a dorsodistal spine; and the ambulatory legs are longitudinally striped in life. The following characters are useful in discriminating among them: development of the rostrum; development and shape of the outer lobe of the maxillule endopod; elongation and armature of the right palm and carpus; armature of the dactyli and propodi of the ambulatory legs; shape of the anterior lobe of the sixth thoracic sternite; armature of the terminal margins of the telson; and coloration in life.

Although the development of the rostrum varies in *P. insulae* and *P. nigrivittatus* sp. nov., it seems constant in *P. pilosipes*, *P. erythrogrammus* sp. nov. and *P. quinquelineatus* sp. nov. Among the latter three species, *P. erythrogrammus* has a most strongly pro-

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Table 1.	Summary of differences among Pagurus pilosipes (Stimpson,	1858), P. insulae Asakura,	1991,	P. erythrogrammus s	sp. nov.,	P. nigrivitt	<i>autus</i> sp.
nov. and	Pagurus quinquelineatus sp. nov.						

Characters	P. pilosipes	P. insulae	P. erythrogrammus	P. nigrivittatus	P. quinquelineatus
Rostrum/interocular lobe	not reaching	variable	reaching	variable	not reaching
Outer lobe of maxillule endopod	recurved	obsolete	recurved	obsolete	recurved
Elongation of right cheliped in males	unknown	strong	moderate	moderate	moderate
Spines on dorsal surface of right palm in males	relatively few, arranged in 5 rows	numerous, scattered	numerous, arranged in 6-8 rows	numerous, scattered	numerous, arranged in 6–8 rows
Carpus of right cheliped	without dorsolateral row of spines	without dorsolateral row of spines	without dorsolateral row of spines	without dorsolateral row of spines	with dorsolateral row of spines
Merus of left cheliped in females	without ventral tubercle	with prominent ventral tubercle	without prominent ventral tubercle	with prominent ventral tubercle	without prominent ventral tubercle
Mesial face of dactylus of second pereopod	unarmed or with 1 or 2 spinules distally	with row of 5–7 spinules dorsally	unarmed or with 1 or 2 spinules distally	unarmed or with 1 or 2 spinules distally	with row of 5–7 spinules dorsally
Mesial face of dactylus	with 1 row of	with 2 rows of	with 1 row of	with 1 row of	with 2 rows of
of third pereopod Number of ventral spines on dactylus of third pereopod	spinules 5-7	spinules 9–13	7–12	5–7	8–14
Ventral spines on dactylus and propodus of left third pereopod	short	short	long	short	long
Lateral surface of propodus of left third percopods in females	unarmed	with rows of small tubercles	unarmed	with rows of small tubercles	unarmed
Ventrodistal lateral angle of propodus of left third percopod	rounded	with spine	rounded	with spine	rounded
Anterior lobe of sixth thoracic sternite	subrectangular	subsemicircular	subsemicircular	subsemicircular	subsemicircular
Terminal margin of telson	with 4 or 5 large spines	with 12–14 small spines or spinules	with 5–8 small spines	with 4 or 5 large spines	with 5–7 small spines
Color of stripes on ambulatory legs	reddish brown	dark brown	reddish brown	dark brown	brick red or reddish brown
Number of stripes on lateral faces of ambulatory propodi	4	3	3	3	5

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duced rostrum reaching the anterior margin of the interocular lobe (Fig. 12A). In *P. pilosipes* and *P. quinquelineatus*, the rostrum does not reach the anterior end of the interocular lobe (Fig. 1A, Fig. 20A).

The outer lobe of the maxillule endopod is recurved in *P. pilosipes, P. erythrogrammus* sp. nov. and *P. quinquelineatus* sp. nov. (Figs. 2A, 12B, 20B), while it is obsolete in *P. insulae* and *P. nigrivittatus* sp. nov. (Figs. 7B, 16B).

The right cheliped of male P. insulae exhibits a tendency toward elongation and toward increase in number and decrease in size of spines on the palm and carpus (Fig. 8A-C). In P. erythrogrammus sp. nov., P. nigrivittatus sp. nov. and P. quinquelineatus sp. nov., the elongation of the right chela in males is moderate (Figs. 13A-D, 17A-C, 21A-D). In P. pilosipes, it remains unknown whether the right chela is elongate in males, because only one male specimen has been available for examination. Spines on the dorsal surface of the right palm are fewer in P. pilosipes (Fig. 3A) than in other four species (Figs. 8A, 9A, 13A, 17A, 18 A, 21A). Furthermore, the spines on the dorsal surface of the right palm are scattered in male P. insulae and male P. nigrivittatus sp. nov., rather than arranged in six to eight irregular rows in P. pilosipes, female P. insulae, female P. nigrivittatus sp. nov., P. quinquelineatus sp. nov. and P. erythrogrammus sp. nov. The carpus of the right cheliped bears a dorsolateral row of small spines in P. quinquelineatus sp. nov. (Fig. 21B), which is absent in other four species (Fig. 3B, 8A, 13A, 17A).

The presence of a prominent tubercle on the ventral surface of the left cheliped merus in females distinguishes *P. insulae* and *P. nigrivittatus* sp. nov. (Figs. 10E, 14B) from the other three species in which the meral tubercle is absent.

The mesial face of the dactylus of the second pereopod is unarmed or armed with only one or two corneous spinules adjacent to the dorsal margin near base of the claw in *P. pilosipes*, *P. erythrogrammus* sp. nov., and *P. nigrivittatus*. (Figs. 5B, 15B, 19B). In *P. insulae* and *P. quinquelineatus*, it bears a row of five to seven corneous spinules adjacent to the dorsal margin (Figs. 11B, 23B). The mesial face of the dactylus of the third pereopod is

armed with two rows of corneous spinules in *P. insulae, P. erythrogrammus* sp. nov. and *P. quinquelineatus* sp. nov. (Figs. 11D, 15D, 23D), rather than having only one short row of corneous spinules in *P. pilosipes* and *P. nigrivittatus* (Figs. 5D, 19D).

Pagurus nigrivittatus sp. nov. and P. pilosipes may be distinguished from P. insulae, P. quinquelineatus sp. nov. and P. erythrogrammus sp. nov. by the fewer ventral spines on the ambulatory dactyli (five to seven versus seven to 14). It should be noted, however, the variation range remains not fully known in P. pilosipes because of the small sample size. Further, the dactylar ventral spines seem to be more elongate in P. pilosipes, P. erythrogrammus sp. nov. and P. quinquelineatus sp. nov. (Figs. 5B, D, 15B, D, 23B, D) than in P. insulae and P. nigrivittatus sp. nov. (Figs. 11B, D, 19B, D).

The ventral spines on the propodi of the third percopods are more elongate in *P. erythro grammus* sp. nov. and *P. quinquelineatus* sp. nov. (Figs. 15D, 23D) than in *P. pilosipes*, *P. insulae* and *P. nigrivittatus* sp. nov. (Figs. 5D, 11D, 19D). Particularly, the spine on the ventrodistal margin is subequal to or longer than the distalmost spines on the dactylar ventral series in the former two species, as opposed to shorter than them in the latter three species. Further, the number of the spines on the left third percopod may be greater in the former two species than the latter three species (three or four versus five to eight).

The propodus of the left third pereopod is armed with rows of small calcareous tubercles on the lateral and ventral surfaces in female P. insulae and P. nigrivittatus sp. nov. (Figs. 11E, 19E). In female P. pilosipes and P. quinquelineatus sp. nov., there are no such tubercles on the propodus of the left third pereopod (Fig. 5C, 23C). In female P. erythrogrammus sp. nov., only the ventral surface is tuberculate (Fig. 23E). Further, the ventrodistal lateral angle of the propodus of the left third percopod is acutely or subacutely pointed in both male and female of P. insulae and P. nigrivittatus sp. nov. (Figs. 11C, E, 19C, E), rather than rounded in the other three species (Figs. 5C, 15C, E, 23C, E).

The anterior lobe of the sixth thoracic ster-

nite is subrectangular in *P. pilosipes* (Fig. 1E), rather than subsemicircular in the other four species (Figs. 6E, 12G, 16G, 20G).

The terminal margin of the telson is armed with four or five large spines in *P. pilosipes* and *P. nigrivittatus* sp. nov. (Figs. 1F, 16H); five to seven small spines in *P. quinquelineatus* sp. nov. (Fig. 20H); five to eight spinules in *P. erythrogrammus* sp. nov. (Fig. 20H); and 12-14 small spine or spinules (two or three spines at the posterolateral angle are calcareous and larger than other corneous spinules) in *P. insulae* (Fig. 6F).

Finally, color and number of the stripes on the ambulatory propodi are different among the five species (Figs. 24, 25). The stripes are reddish brown or brick red in P. pilosipes, P. erythrogrammus sp. nov. and P. quinquelineatus sp. nov., while they are dark brown in P. insulae and P. nigrivittatus sp. nov. The stripes which are visible in the lateral view are three in P. insulae, P. erythrogrammus sp. nov. and P. nigrivittatus sp. nov. (the ventral stripe is sometimes rather obscure in P. nigrivittatus sp. nov.); four in P. pilosipes; and five in *P. quinquelineatus* sp. nov. In general coloration, P. insulae and P. nigrivittatus sp. nov. are very similar. However, the dorsal stripe on the ambulatory propodus reaches to the distal margin of the propodus in *P. insulae* (Fig. 24E), rather than not reaching in P. nigrivittatus sp. nov. (Fig. 25D).

Discussion

Despite the general similarities in morphology and coloration, it remains unclear whether the five species treated in this study are really closely related. For example, the carpus of the right second pereopod has just a dorsodistal spine in these five species, but that is also true of other congeneric species, i. e. species of the provenzanoi and anachoretus groups (Lemaitre et al., 1982; McLaughlin and Haig, 1993; McLaughlin and Forest, 1999), and P. exiguus Melin, 1939 (McLaughlin and Sandberg, 1995). The dorsally unarmed propodus of the right second pereopod is also found in various congeneric species, i. e. species of the provenzanoi and anachoretus groups (Lemaitre et al., 1982; McLaughlin and Haig, 1993; McLaughlin and Forest, 1999), P. exiguus (see McLaughlin and Sand-

berg, 1995), P. imafukui McLaughlin and Konishi, 1994 (McLaughlin and Konishi, 1994), P. lanuginosus De Haan, 1849 and P. maculosus Komai and Imafuku, 1996 (Komai and Imafuku, 1996). The striped ambulatory legs are shared by a number of congeneric species, i.e. species of the provenzanoi and anachoretus groups (i.e. Haig and McLaughlin, 1991; Harvey and McLaughlin, 1991; McLaughlin and Forest, 1999), P. minitus Hess, 1865 (Komai and Mishima, in press) and P. proximus Komai, 2000 (Komai, 2000). Furthermore, some of the characters distinguishing among the five species commonly differentiate groups within the genus, i.e. the development of the external lobe of the maxillule endopod, the armature of the dactylus and propodus of the left third pereopod and the shape and armature of the telson (McLaughlin, 1974). Phylogenetic relationships among species of Pagurus remain little studied, although the heterogeneity of the genus have been suggested (i.e. McLaughlin, 1997). Therefore, it is difficult to comment further on the phylogenic relationships among the five species.

As previously mentioned, Stimpson's (1858) original description of Pagurus pilosipes was brief, and included general characters of many species of *Pagurus* occurring in shallow waters in the northwestern Pacific. The spinose chelae and the red-striped color pattern of the ambulatory legs, noted by Stimpson, are possessed by the two new species described in this study (P. quinquelineatus and P. erythrogrammus spp. nov.). However, besides P. pilosipes, no other pagurid species having such characteristics have been reported from the subtropical Ryukyu Islands (Minei, 1973; unpublished data). The neotype from the topotypic locality fixed the specific identity of P. pilosipes.

It has been found that reports of *Pagurus* (or *Eupagurus*) *pilosipes* subsequent to the original description by Stimpson (1858; see also 1907) (Miyake, 1978, 1982; Miyake and Imafuku, 1980; Oh, 1983; Takeda, 1986; Asakura, 1991, 1995; Wang, 1992, 1994; Minemizu, 2000) can not be referred to the true *P. pilosipes*. References by Alcock (1905), Terao (1913) and Gordan (1956) are merely bibliographic treatments.

T. Komai



Fig. 24. Semi-diagrammatic figures of second pereopods, showing color pattern on lateral surface. A, *Pagurus pilosipes* (Stimpson, 1858); B, *Pagurus insulae* Asakura, 1991 (only dactylus and propodus are shown); C, *Pagurus erythrogrammus* sp. nov.; D, *Pagurus nigrivittatus* sp. nov.; E, *Pagurus quinquelineatus* sp. nov.





Fig. 25. A, *Pagurus erythrogrammus* sp. nov., paratype male (sl 4.0 mm; CMNH-ZC 628) (photo taken by J. Okuno); B, *Pagurus nigrivittatus* sp. nov., paratype male (sl 4.0 mm; CMNH-ZC 1009) (photo taken by J. Okuno); *Pagurus quinquelineatus* sp. nov., paratype female (sl 3.1 mm; CBM-ZC 6622).

Miyake (1978) reported *P. pilosipes* based upon Japanese specimens from Sagami Bay, Seto Inland Sea, and East China Sea. Twentyone of 24 lots used by him were located and used in this study. Two specimens from Sagami Bay (Miyake det. no. 263, 549) and two lots containing a total of seven specimens from the Seto Inland Sea (ZLKU 8958, 16835) were not located. Results of the reidentification are summarized in Table 2. Six species in three genera were confounded in Miyake's (1978) material of P. pilosipes, of which none represents the true *P. pilosipes*. Seven specimens (Miyake det. no. 385, 388, 408, 409, 411, 416 and 455) are referred to *Pagurus erythrogrammus* sp. nov. Four specimens in the three lots (Miyake det. no. 387, 395 and 471) have been identified as *P. quinquelineatus* sp. nov. As Komai and Osawa (2001) indicated, one specimen (Miyake det. no. 398)

Miyake det. no.	Reg. no.	Re-identitication
263	unknown	not located
385	NSMT-CrR 1803	Pagurus erythrogrammus sp. nov.
387	NSMT-CrR 1805	Pagurus quinquelineatus sp. nov.
388	NSMT-CrR 1806	Pagurus erythrogrammus sp. nov.
395	NSMT-CrR 1813	Pagurus quinquelineatus sp. nov.
398	NSMT-CrR 1816	Pagurus decimbranchiae Komai and Osawa, 2001
408	NSMT-CrR 1826	Pagurus erythrogrammus sp. nov.
409	NSMT-CrR 1827	Pagurus erythrogrammus sp. nov.
410	NSMT-CrR 1828	Pagurus quinquelineatus sp. nov.
411	NSMT-CrR 1829	Pagurus erythrogrammus sp. nov.
416	NSMT-CrR 1834	Pagurus erythrogrammus sp. nov.
454	NSMT-CrR 1964	Nematopagurus sp.
455	NSMT-CrR 1965	Pagurus erythrogrammus sp. nov.
471	NSMT-CrR 2020	Pagurus quinquelineatus sp. nov.
490	NSMT-CrR 2068	Propagurus obtusifrons (Ortmann, 1892)
549	unknown	not located
559	NSMT-CrR 2254	Pagurus quinquelineatus sp. nov.
627	NSMT-CrR 3533	Pagurus proximus Komai, 2000
_	ZLKU 8958	not located
—	ZLKU 16835	not located
_	ZLKU 8759	Nematopagurus sp.
—	ZLKU 8765	Nematopagurus sp.
—	ZLKU 8769	Nematopagurus sp.
_	ZLKU 8775	Nematopagurus sp.

Table 2. Results of re-identifications of the specimens referred to Pagurus pilosipes by Miyake (1978).

is Pagurus decimbranchiae Komai and Osawa, 2001. One small specimen (Miyake det. no. 490) has no trace of gonopores on either third or fifth pereopods, and thus is considered to be a juvenile. Because of the presence of distinctly quadriserial gills, this specimen is provisionary identified as Propagurus obtusifrons (Ortmann, 1892) (see Komai and Yu, 1999). Another specimen (Miyake det. no. 627) has been found to represent Pagurus proximus Komai, 2000. One specimen from Sagami Bay (Miyake det. no. 454) and four specimens from the East China Sea (ZLKU 8759, 8765, 8769 and 8775), all females, are identified as Nematopagurus sp. because of the widely separated ocular acicles and the possession of paired first pleopods. The genus *Nematopagurus* A. Milne-Edwards and Bouvier, 1892 is under review by Dr. Patsy A. McLaughlin (McLaughlin, in press), and the definite identification will be made after her paper is published.

Miyake (1978) noted that the four specimens from Onomichi, Seto Inland Sea (ZLKU 16835) were collected from the *Zostera* zone. It is highly likely that the four specimens actually represent *Pagurus minutus* (Hess, 1865), which is the most common species of *Pagurus* in shallow tidal flat areas, including *Zostera* beds, in local waters (Komai and Mishima, in press). None of the five species treated in this paper occurs in tidal or subtidal flats. Additionally, the fact that *P. minutus* also has striped ambulatory legs (the propodi bear a dark gray-brown median stripe on each lateral face) would seem to support this assumption.

The illustrations given by Miyake (1978, text-fig. 34) are confusing, as they are not consistent with any species reidentified here. The right cheliped illustrated by Miyake (text-figure 34c) is apparently similar to that of *Nematopagurus* sp., particularly in the presence of a row of spines on the dorsal mid-line of the right chela. However, the shield and cephalic appendages illustrated (Miyake, 1978, text-fig. 34a) most resemble those of *Pagurus erythrogrammus* sp. nov., particularly regarding the well produced rostrum. The armature and color pattern of the pereopod illustrated (Miyake, 1978, text-fig. 34d) are generally similar to those of *P. quinque*

lineatus sp. nov. The telson (Miyake, 1978, text-fig. 34e) does not agree with any species mentioned. There is no doubt that Miyake's (1978) illustrations were based on more than one species.

Miyake and Imafuku (1980) reported and illustrated *Pagurus pilosipes* from the Kii Peninsula. Their specimens have been reexamined, and found to represent another species, *Pagurus nigrivittatus* sp. nov. Miyake (1982, 1991, 1998) illustrated this species again as *P. pilosipes*. Subsequent workers reporting *P. pilosipes* (e.g., Asakura, 1991, 1995; Minemizu, 2000) followed Miyake and Imafuku's (1980) and Miyake's (1982) identifications.

Oh (1983) recorded *P. pilosipes* from Mara Islet, Korea. Although Oh's specimens were not available for reexamination, there is little doubt that his specimens represent *P. nigrivittatus* sp. nov. He clearly mentioned that the second pereopod had six or seven ventral spines on the dactylus and only three ventral spines on the propodus in his specimens. Further, the color pattern of his specimen illustrated (Oh, 1983, pl. 3, figs. 3, 4) is consistent with that of *P. nigrivittatus* sp. nov.

Wang (1992, 1994) listed *P. pilosipes* from China. Unfortunately, no specimens from China, which are referable to *P. pilosipes* s.l., have been available for study. Nevertheless, it is most probable that Wang was basing his identification on Miyake's (1978, 1982) accounts. Therefore, the references of Wang (1992, 1994) were not referred to *P. pilosipes*.

Matsukubo (1999) published a photograph of a live specimen which he referred to *Pagurus dubius* (Ortmann, 1892). However, judging from the coloration and locality, the specimen is assigned to *P. nigrivittatus* sp. nov. without doubt.

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Pagurus pilosipes (Stimpson)の再検討, P. insulae Asakura の補足的記載, および東アジア海域産ホンヤドカリ属 3新種の記載(甲殻綱:十脚目: 異尾下目:ホンヤドカリ科)

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日本および台湾から採集された標本に基づいてホン ヤドカリ科の Pagurus pilosipes (Stimpson, 1858)の 分類学的再検討を行った.本種は、沖縄本島から採集 された標本に基づいて記載され、その後本州各地、韓 国、中国沿岸から報告されてきたが、原記載以来、タ イプ産地である沖縄からの報告例はなかった. Miyake (1978) と三宅・今福 (1980) により Pagurus pilosipes と同定された標本を再検討した結果, Miyake (1978) により本種と同定された標本には6 種のホンヤドカリ科ヤドカリ類が混在しており(その うち4種は既知種に同定された,さらに三宅・今福 (1980) により本種と同定された標本は前者に含まれ る6種のいずれとも異なることが判明した.種の位置 が不明確な3種の位置を決定するために、沖縄本島か ら採集された P. pilosipesの原記載によく一致する標

本との比較を行った結果,本州産の3種のいずれも沖 縄産の標本とは異なることが判明した. さらに, P. pilosipes と近縁であるとして記載された P. insulae Asakura, 1991 (ムニンタテジマホンヤドカリ)のタ イプ標本を再検討したところ、原記載では言及されて いない鉗脚や歩脚の顕著な変異の存在が判明した. さ らにこれらの変異のため、原記載において近縁種との 識別に用いられた形態形質のほとんどが種の識別形質 として有効でないことが判明した. そこで, P. insulae も含めて検討を進めたところ、上記の3種はいずれも 未記載種であるという結論に達し、新種 P. erythrogrammus, P. nigrivittatus, および P. quinquelineatus と命名した. Pagurus pilosipes と3新種については 詳細な記載と図を与え、P. insulae については、補足 的な記載を与えた. また, P. insulae の原記載で与え られた図は触角棘の形状、口器の形態、右鉗脚の棘の 密度や形状など多くの点で標本との不一致が認められ たので、新たに詳細な図を与えた. さらに、5種間の 識別形質について論議し、分類学的な混乱の解決を 行った.

本論文で扱った5種のいずれも潮間帯~浅海の岩 礁に生息するが, *P. erythrogrammus* は水深75 m か ら記録された.現在のところ, *P. pilosipes* と*P. in*- sulae はそれぞれ沖縄本島と小笠原諸島から知ら れるだけであるが, P. quinquelineatus, P. erythrogrammus, P. nigrivittatus の3新種は日本沿岸の暖温 帯域(房総半島以南の大平洋沿岸と,日本海南部沿岸) に分布する. さらに, P. nigrivittatus は台湾東北部か らも記録された.

従来, Pagurus pilosipes にはアカシマホンヤドカリ という和名が与えられてきた (Miyake, 1978). これは 原記載で Stimpson (1858) が、本種の歩脚に赤い縦縞 模様があることに言及している上, Miyake (1978) が 同定した材料に混在している種のうち、本論文で記載 された2新種が赤褐色系の縦縞模様を歩脚に持って いることに起因しているものと考えられる.しかし, その後,三宅(1982)以降の図鑑やフィールドガイド では、黒褐色の縦縞模様を持つ Pagurus nigrivittatus がアカシマホンヤドカリと呼ばれている. このような 矛盾と混乱を解消するために、以下のように和名を提 唱したい: Pagurus pilosipes オキナワアカシマホンヤ ドカリ (新称), Pagurus erythrogrammus sp. nov. ア カシマホンヤドカリ, Pagurus nigrivittatus sp. nov. クロシマホンヤドカリ (新称), Pagurus quinquelineatus sp. nov. ゴホンアカシマホンヤドカリ (新称).