Benthos Research Vol. 58, No. 1 : 15 - 30 (2003)

BENTHOS RESEARCH
The Japanese Association of Benthology

A Redescription of *Pagurus minutus* Hess, 1865, a Senior Synonym of *Pagurus dubius* (Ortmann, 1892) (Crustacea: Decapoda: Anomura: Paguridae)

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Abstract: The lectotype of *Pagurus minutus* Hess, 1865 and the syntypes of *Pagurus dubius* (Ortmann, 1892) were compared. *Pagurus minutus* has proved to be a senior subjective synonym of *Pagurus dubius*. Hess's species is redescribed and illustrated in detail based on the type material and an abundance of additional specimens from Japan, Korea, and Taiwan. Notable intraspecific variations are seen in the right cheliped and dissimilarity of the third pereopod. In males, a tendency toward elongation of the right cheliped accompanied with reduction of the armature is found. The degree of dissimilarity in the third pereopods is stronger in females than in males. *Pagurus minutus* is most similar to *P. filholi* (De Man, 1887) and *P. samuelis* (Stimpson, 1858). The elongate dactyli of the second and third pereopods and the coloration in life immediately distinguish *P. minutus* from these other two species.

Key words: Crustacea, Decapoda, Anomura, Paguridae, *Pagurus minutus, Pagurus dubius,* synonym, redescription, East Asia

INTRODUCTION

Pagurus dubius (Ortmann, 1892) is known as one of the most common hermit crabs in East Asian waters, mainly inhabiting tidal flats and adjacent areas of estuarine or marine environments. It was described by Ortmann (1892) based on an abundance of specimens collected from Tokyo Bay by L. Döderlein. Since the original description, the species has been reported from Japan (including the Ryukyu Islands), the Russian Far East, Korea, China, and Taiwan (e.g., Makarov 1938, 1962; Vinogradov 1950; Miyake 1957, 1975, 1978, 1982; Minei 1973; Takeda 1982; Yu & Foo 1990; Komai et al. 1992; Asakura 1995). Despite its commonness, a fully detailed description of the species has not been published.

Received November 25, 2002: Accepted April 7, 2003
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Prior to Ortmann (1892), Hess (1865) had described a new species of hermit crab, *Pagurus minutus*. The type locality for *P. minutus* was given as Sydney, Australia. Hess's original description was cryptic. De Man (1887) presented a critical review of Hess's (1865) work, based upon his own reexamination of all of Hess's material housed at that time in the Göttingen Museum, Germany. Of the hermit crab species described by Hess, De Man (1887) concluded that Hess had confounded two species under the name *P. minutus*. De Man redescribed and illustrated *P. minutus* (as *Eupagurus*) based on one of the two syntypes, and described the second specimen as new under the name *Eupagurus filholi*. Since De Man (1887), *Pagurus minutus* had been mentioned in the bibliographic compilations of Alcock (1905) and Gordan (1956). Sandberg & McLaughlin (1993) redescribed and illustrated the lectotype of *P. minutus* and the holotype of *P. filholi*, and suggested that the collecting locality for the specimens indicated by Hess (1865) was probably incorrect.

During the course of revisionary studies of species of *Pagurus* in the northwestern Pacific, the lectotype of *P. minutus*, currently housed in the collection of the Swedish Museum of Natural History, and the syntypes of *P. dubius* deposited in the collection of the Musée Zoologique de Strasbourg, were examined. Abundant samples from other sources have also been available for study. It has been found that *P. minutus* and *P. dubius* are conspecific, and that the syntypes of *P. dubius* include specimens of the sympatrically occurring diogenid *Diogenes nitidimanus* Terao, 1913. Consequently, a lectotype is selected for *P. dubius* in the interest of nomenclatural stability. The name *Pagurus minutus* has priority over *Pagurus dubius*, although the latter name is far more familiar than the former. The redescription of *P. minutus* given by Sandberg & McLaughlin (1993) was based only on a male lectotype, and no detailed description of *P. dubius* has been published. Thus intraspecific variation of the species remains little known. We provide here a full redescription of the species for completeness and for adequate comparison with the close relatives *P. samuelis* (Stimpson, 1858) and *P. filholi* (De Man, 1887).

MATERIALS AND METHODS

Specimens used for this study are deposited in the Natural History Museum and Institute, Chiba, Japan (CBM); Kitakyushu Museum of Natural History and Human History, Kitakyushu, Japan (KMNH); Musée Zoologique, Strasbourg, France (MZS); National Taiwan Ocean University, Keelung, Taiwan, R.O.C. (NTOU); Swedish Museum of Natural History, Stockholm, Sweden (SMNH); and Zoologische Staatssammlung München, Germany (ZSM). General terminology used in the description follows McLaughlin (1974), with exception of the posterior carapace (see Lemaitre 1995), fourth pereopod (see McLaughlin 1997), and gill structure (see McLaughlin & de Saint Laurent 1998); the term "paragastric grooves" is used following Komai & Osawa (2001). One measurement, shield length (sl), measured in millimeters (mm) from the tip of the rostrum or midpoint of the rostral lobe to the midpoint of the posterior margin of the shield, provides an indication of size of the specimens examined. Illustrations were made with the aid of a drawing tube mounted on a Leica MZ-8 stereomicroscope.

TAXONOMIC ACCOUNT

Family Paguridae
Genus *Pagurus* Fabricius, 1775

Pagurus minutus Hess, 1865
(Figs. 1–6)

Pagurus minutus Hess, 1865: 180 (part) [type locality: Sydney (probably in error, see "Discussion")]; Haswell, 1882: 156 (part); Gordan, 1956: 332; Sandberg & McLaughlin, 1993: 219, figs 2, 4; Davie, 2002: 84.

Eupagurus minutus - De Man, 1887: 705, fig. 2; Alcock, 1905: 175.

Eupagurus dubius Ortmann, 1892: 307 (part), pl. 12, fig. 12, 14k [type locality: Tokyo Bay]; Doflein, 1902: 646; Alcock, 1905: 117 (list); Balss, 1913: 55.

Eupagurus similis - Doflein 1902: 646. Not *Eupagurus similis* Ortmann, 1892. See "Discussion."

Eupagurus samuelis - Terao, 1913: 371 (part). Not *Pagurus samuelis* (Stimpson, 1858).

?*Eupagurus dubius* - Yokoya, 1939: 284. See "Discussion."

Pagurus dubius - Derjugin & Kobjakova, 1935: 142; Vinogradov, 1950: 227, fig. 119; Gordan, 1956: 329 (list); Miyake, 1957: 87; 1960: 90, pl. 45, fig. 8; 1961a: 12; 1961b: 169; 1965: 647; 1975: 326, pl. 115, fig. 4; 1978: 99, fig. 38, pl. 1, fig. 6; 1982: 127, pl. 43, fig. 2; 1991: 127, pl. 43, fig. 2; 1998: 127, pl. 43, fig. 2; Miyake et al., 1962: 125; Kim, 1963: 300, fig. 17; 1964: 9; 1970: 8; 1973: 227, fig. 51, pl. 70, fig. 31a, b; Kobjakova, 1967: 241; Suzuki, 1971: 97, pl. 34, fig. 2; Minei, 1973: 46; Miyake & Imafuku, 1980: 60; Takeda, 1982: 67, fig. 200; Komai et al., 1992: 197; Wang, 1994: 570; Asakura, 1995: 363, pl. 97, fig. 10.

?*Pagurus dubius* - Makarov, 1938: 188, pl. 3, fig. 5; Makarov, 1962: 178, pl. 3, fig. 5. See "Discussion."

Not *Eupagurus minutus* - Makarov, 1938: 320 [misspelling of *Pagurus munitus* (Benedict, 1892) = *Elassochirus gilli* (Benedict, 1892)].

Not *Eupagurus dubius* - Yokoya, 1933: 81. See "Discussion."

Not *Pagurus dubius* - Igarashi, 1970: 5, pl. 3, fig. 10. = ?*Pagurus trigonocheirus* (Stimpson, 1858). See "Discussion."

Not *Pagurus dubius* - Yu & Foo, 1990: unnumbered fig. See "Discussion."

Not *Pagurus dubius* - Matsukubo, 1999: 170,

unnumbered fig., 284. See "Discussion."
Not *Pagurus dubius* - Minemizu, 2000: 150. = *Pagurus proximus* Komai, 2000. See "Discussion."

Type material. Lectotype of *Pagurus minutus* Hess, 1865 (selected by De Man 1887): The type locality was originally indicated as Sydney by Hess (1865), but the real locality is unknown, male (sl 4.2 mm) (SMNH-Type 4377).

Lectotype of *Pagurus dubius* (Ortmann, 1892) (herein selected): Tokyo Bay, 1882, coll. L. Döderlein, male (sl 5.4 mm) (MZS 476A). Paralectotypes: same data as lectotype, 1 male (sl 5.9 mm) (MZS 476B); same data as lectotype, 83 specimens (largest male sl 5.5 mm) (MZS 476C).

Other material. Japan. Tohoku District: Ohtsuchi Bay (Nebama Beach), Iwate Prefecture, *Zostera* beds, 3 −4 m, 26 May 1995, beam trawl, coll. T. Komai, 8 males (sl 2.5−5.8 mm) (CBM-ZC 1696). Tokyo Bay: Yokohama, 1 male, 1 female (not measured), referred to *Eupagurus similis* Ortmann, 1892 by Doflein (1902) (ZSM 303/1); Kaneda Beach, Kisarazu, sand flat, intertidal, 8 May 2000, hand, coll. T. Komai, 2 males (sl 5.6, 6.0 mm) (CBM-ZC 6473). Boso Peninsula: Takeoka Fishing Port, 2−3 m, 7 May 1994, trap, coll. T. Komai, 1 male (sl 4.1 mm) (CBM-ZC 448); Takeoka Beach, Futtsu, rocky bottom, intertidal, 25 June 1994, hand, coll. T. Komai, 10 males (sl 2.9−6.1 mm), 3 females (sl 3.4 − 3.8 mm) (CBM-ZC 541); Kazusa Minato-gawa rivermouth, muddy bottom, intertidal, 20 Sept 2002, hand, coll. T. Komai, 3 males (sl 3.1−5.3 mm) (CBM-ZC 6507). Kii Peninsula: Kushimoto (Hashikui Beach), sand flat, intertidal, 3 Feb 1995, hand, coll. T. Komai, 10 males (sl 3.9 − 7.2 mm). Shikoku: Uchinoura Bay, Usa, Kochi Prefecture, sand flat, subtidal, 22 Sept 1999, hand, coll. H. Endo, 1 male (sl 4.9 mm) (CBM-ZC 5215); Iyono-gawa rivermouth, Sukumo, Kochi Prefecture, 6 June 2000, hand, coll. K. Nomura, 2 males (sl 3.9, 4.8 mm) (CBM-ZC 5503). Seto Inland Sea: Chigusa-gawa rivermouth, Ako, Hyogo Prefecture, intertidal, 27 Apr 1997, hand, coll. K. Nomura, 1 male (sl 3.3 mm) (CBM-ZC 6474). Noto Peninsula (Sea of Japan): Noto, intertidal, 9 Oct 1988, 1 male (sl 4.1 mm) (CBM-ZC 874). Kyushu: Bansho-gawa rivermouth, Saiki, Oh-ita Prefecture, intertidal, 7 Nov 1994, hand, coll. T. Komai, 1 male (sl 2.8 mm), 1 female (sl 2.9 mm) (CBM-ZC 902); Gotanda-gawa rivermouth, Kushikino, Kagoshima Prefecture, intertidal, 5 Apr 1999, hand, coll. T. Komai, 3 males (sl 3.3−4.7 mm) (CBM-ZC 5151); Mitoma, Fukuoka, Fukuoka Prefecture, intertidal, 26 June 1994, hand, coll. S. Mishima, 2 females (sl 2.5, 3.2 mm) (CBM-ZC 6476); same locality, intertidal, 22 Sept 2001, hand, coll. S. Mishima, 1 male (sl 4.4 mm) (CBM-ZC 6478); same locality, intertidal, 1 Oct 2001, hand, coll. S. Mishima, 1 male (sl 4.5 mm) (CBM-ZC 6477); same locality, rubble area, intertidal, 3 Dec 2001, hand, coll. S. Mishima, 2 males (sl 5.0, 5.3 mm) (CBM-ZC 6479); same locality, intertidal, 8 July 2001, hand, coll. S. Mishima, 1 male (sl 3.6 mm) (KMNH IvR 400007); Nokonoshima Island, Fukuoka, Fukuoka Prefecture, intertidal, 6 Sept 1992, hand, coll. S. Mishima, 1 male (sl 5.8 mm), 2 females (sl 4.8, 4.9 mm) (KMNH IvR 400001−400003); Shioya-bana Peninsula, Fukuoka, Fukuoka Prefecture, intertidal, 16 Oct 1993, hand, coll. S. Mishima, 1 female (sl 2.9 mm) (KMNH IvR 400004); Makino-hana Peninsula, Fukuoka, Fukuoka Prefecture, intertidal, 30 Jan 1998, hand, coll. S. Mishima, 2 ovigerous females (sl 2.4, 2.9 mm) (KMNH IvR 400005−400006); same locality, intertidal, 20 Jan 2002, hand, coll. S. Mishima, 1 female (sl 3.1 mm) (KMNH IvR 400012); same locality, intertidal, 3 Dec 2001, hand, coll. S. Mishima, 1 male (sl 7.4 mm) (KMNH IvR 400011); Wakana-gawa rivermouth, Mogi, Nagasaki Prefecture, intertidal, 15 Sept 2001, hand coll. S. Mishima, 3 males (sl 4.7−5.1 mm) (KMNH IvR 400008−400010); Amura, Amakusa, Kumamoto Prefecture, sand flat, intertidal, 31 Mar 2002,

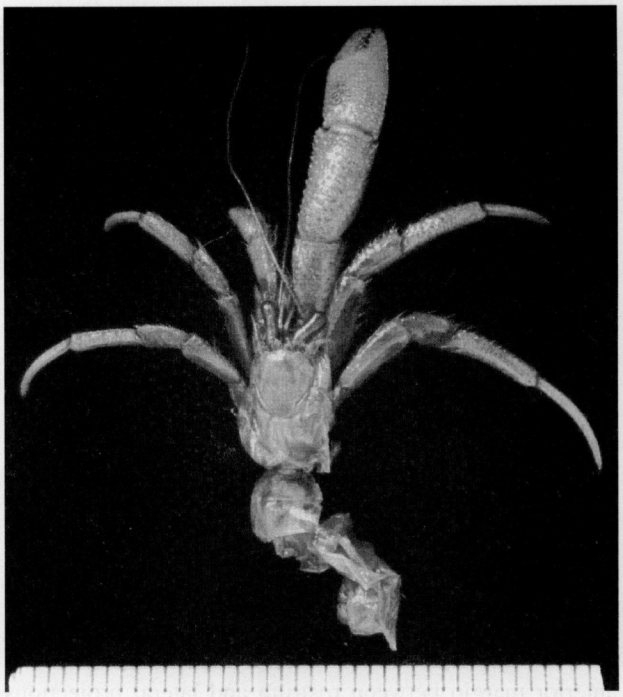

Fig. 1. *Pagurus minutus* Hess, 1865. Lectotype of *Pagurus dubius* (Ortmann, 1892), male (sl 5.4 mm) from Tokyo Bay, entire animal in dorsal view.

2 males (sl 3.7－4.5 mm) (KMNH IvR 400013-400014). Ryukyu Islands: Kitanakagusuku, Okinawa Island, sand flat, intertidal, 23 June 1994, hand, coll. T. Komai, 6 males (sl 2.5－4.8 mm) (CBM-ZC 921).

Korea. Kunsan, tide pool, 16 Oct 1999, hand, coll. F. Muto, 1 male (sl 5.9 mm) (CBM-ZC 5506); northern Anmyondo, Taean, intertidal, 22 Dec 2002, hand, coll. S. Mishima, 1 male (sl 3.6 mm) (KMNH IvR 400015); Chanri, Cheonsuman, Taean, intertidal, 22 Dec 2002, hand, coll. S. Mishima, 1 female (sl 4.5 mm) (KMNH IvR 400016).

Taiwan. Chang-Hua County, western Taiwan, mudflat, intertidal, 30 Nov 1996, hand, coll. T.-Y. Chan, 1 ovigerous female (sl 5.9 mm) (NTOU); mudflat, intertidal, 12 Mar 1997, hand, 1 male (sl 4.7 mm) (NTOU).

Redescription. Eleven pairs of biserial phyllobranchiae.

Shield (Fig. 2A) 1.0－1.1 times as long as broad; anterior margin between rostrum and lateral projections weakly concave; anterolateral margins sloping; posterior margin roundly truncate; dorsal surface with several pair of tufts of setae laterally and 2 median tufts (one at base of rostrum); paragastric grooves inconspicuous; rostrum rounded or triangular, occasionally terminating in tiny spinule, reaching to or beyond lateral projections; lateral projections obtusely triangular, with or without submarginal spinule. Posterior carapace (Fig. 2B) subequal in length to shield, generally membranous (except for weakly calcified anterior part of posteromedian plate), with numerous scattered tufts of short to long setae; cardiac sulci nearly reaching posterior margin of carapace, weakly diverging posteriorly; sulci cardiobranchialis parallel to cardiac sulci, reaching level of midlength of posterior carapace.

Ocular peduncles (Fig. 2A) 0.7－0.9 times as long as shield, weakly inflated basally, with sparse tufts of short setae dorsomesially; corneas slightly dilated. Ocular acicles moderately separated basally, each subovate with sharply edged mesial margin, bearing small submarginal spine; dorsal surface slightly concave, with tuft of setae. Interocular lobe clearly visible in dorsal view, with concave anterior surface.

Antennular peduncles (Fig. 2A), when fully extended, reaching or slightly overreaching distal margins of corneas. Basal segment moderately inflated laterally, unarmed on lateral face of statocyst lobe. Ultimate segment 1.4－1.6 times as long as penultimate segment, slightly broadened distally in lateral view, with row of sparse, short setae on dorsal surface.

Antennal peduncles (Fig. 2A) reaching or slightly overreaching distal margins of corneas. First segment with or without spinule on lateral surface distally; ventrodistal margin with 1 spinule laterad of antennal gland opening. Second segment with dorsolateral distal angle produced, reaching to 0.3－0.5 of fourth segment, terminating in simple or bifid spine; dorsomesial distal angle with spinule. Third segment with spinule at ventromesial distal angle. Fourth and fifth segments with scattered setae or tufts of setae. Antennal acicle moderately short, reaching at least to base of cornea, but not overreaching distal margin, with row of stiff setae on mesial face. Antennal flagellum long, reaching to tip of forwardly extended right cheliped, with 2－4 minute setae every 1 or 2 articles.

Mandible (Fig. 3A) with 3 blunt or subacute teeth distally and 1 acute tooth subproximally on mesial margin of incisor process; distal segment of palp relatively long and slender. Maxillule (Fig. 3B) with broad, subquadrate coxal endite; endopod broad, inner lobe weakly produced with 1 apical bristle, outer lobe obsolete. Maxilla (Fig. 3C) with anterior lobe of scaphognathite not reaching distal margin of distal lobe of basial endite; endopod slightly overreaching distal margin of anterior lobe of scaphognathite. First maxilliped (Fig. 3D) with moderately broad exopod. Second maxilliped (Fig. 3E) with moderately broad endopod; exopod moderately broad. Third maxilliped (Fig. 3F) with moderately slender endopod; ischium (Fig. 3G) with crista dentata well developed, composed of corneous or corneous-tipped teeth increasing in size proximally, and with 1 accessory tooth; merus devoid of ventromesial and dorsodistal spines; carpus without dorsodistal spine; propodus increasing in depth distally; dactylus 0.5－0.6 times as long as propodus; exopod moderately slender, slightly overreaching distal margin of merus.

Right cheliped of males (Figs. 4A, B, 5A, B) appreciably larger than left, showing tendency toward elongation and reduction of armature. Chela length attaining 2.0 times width, subovate to elongate subovate in general outline in dorsal view; fingers depressed dorsoventrally; narrow hiatus between fingers. Dactylus slightly shorter than to equal to length of palm; dorsal surface flat or slightly convex, with 2 rows of tufts of short setae and conspicuous row of small spines mesiad of midline; dorsomesial margin with distinct, tuberculate or denticulate ridge; mesial face with row of small spines dorsally; ventral surface with rows of short setae; cutting edge with row of blunt, calcareous teeth decreasing in size distally, terminating in small, corneous claw. Palm slightly shorter than carpus; dorsal surface convex (reduction of

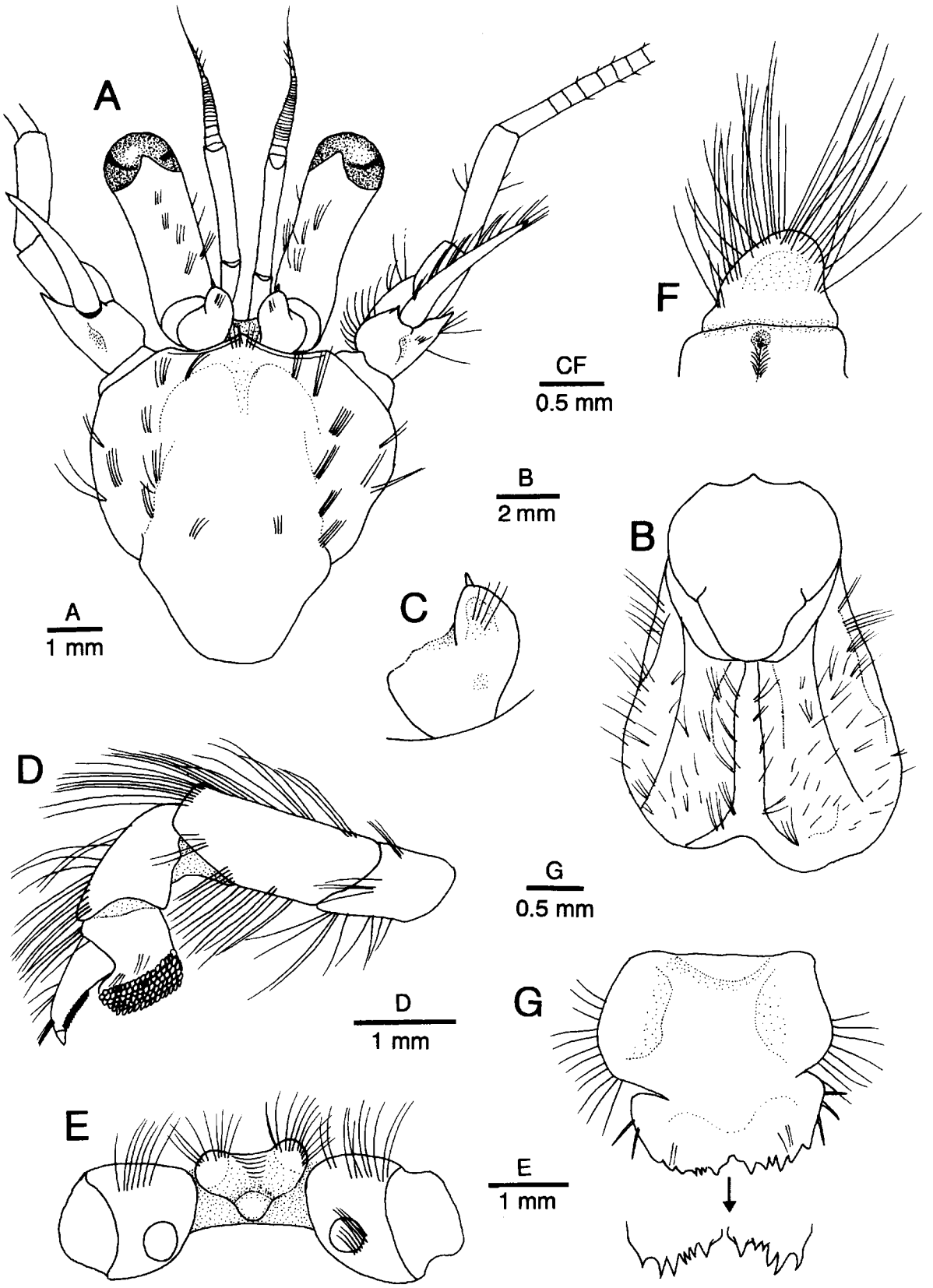

Fig. 2. *Pagurus minutus* Hess, 1865. A, shield and cephalic appendages, dorsal (setae on left antenna omitted); B, carapace, dorsal; C, left ocular acicle, dorsal; D, left fourth pereopod, lateral; E, coxae of fifth pereopods, eighth thoracic sternite, ventral; F, anterior lobe of sixth thoracic sternite, ventral; G, telson, dorsal; inset, terminal margins, posterodorsal. A-C, E, G, male (sl 6.0 mm; CBM-ZC 6473) from Kaneda Beach, Kisarazu, Tokyo Bay; D, F, lectotype male (sl 4.2 mm; SMNH-Type 4377) from unknown locality.

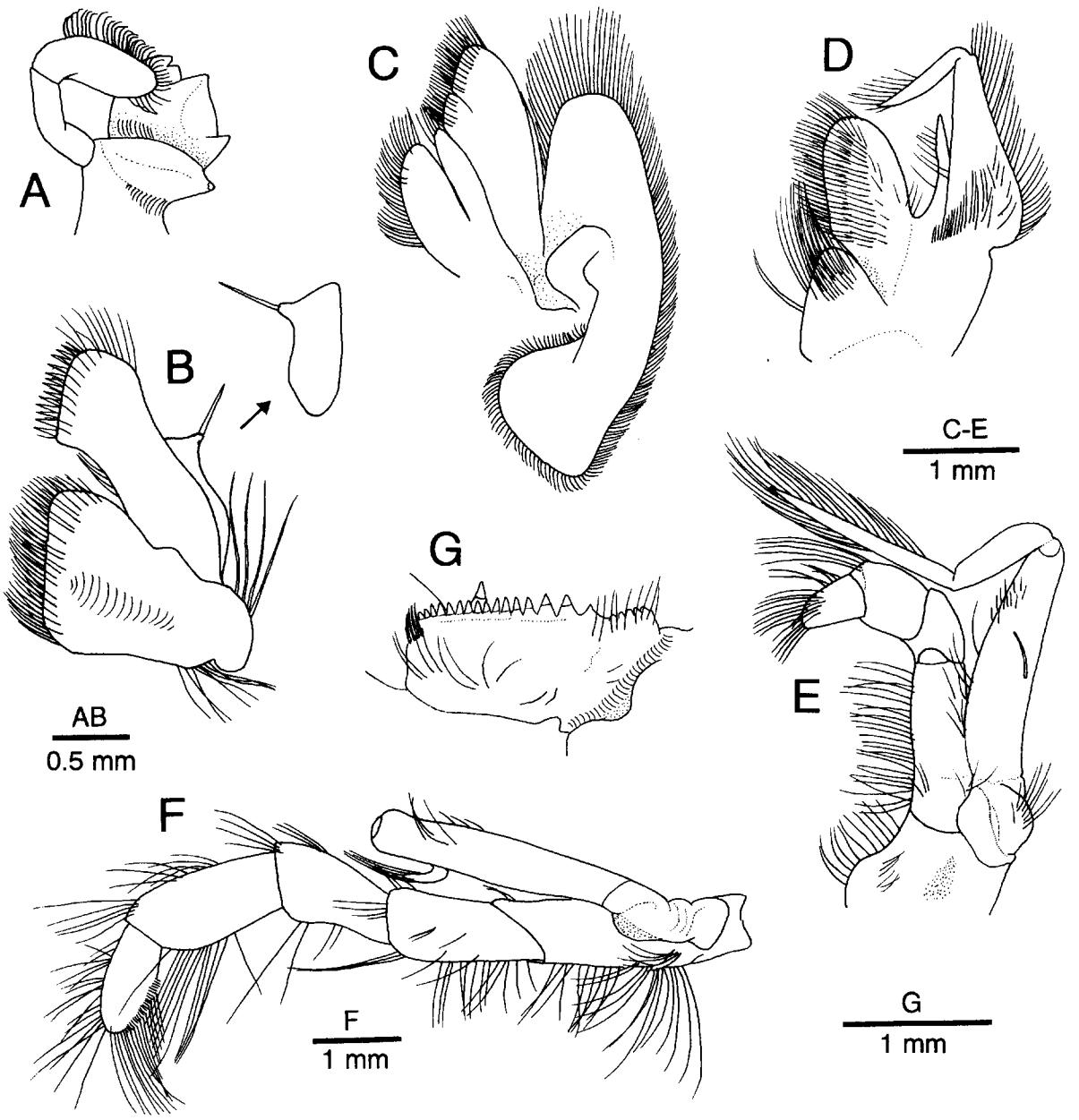

Fig. 3. *Pagurus minutus* Hess, 1865. Left mouthparts. A, mandible, dorsal; B, maxillule, ventral; inset, endopod, lateral; C, maxilla, ventral; D, first maxilliped, ventral; E, second maxilliped, ventral; F, third maxilliped, lateral; G, ischium of third maxilliped, dorsal (setae omitted). Male (sl 6.0 mm; CBM-ZC 6473) from Kaneda Beach, Kisarazu, Tokyo Bay.

convexity apparently correlated to elongation of right cheliped), covered with numerous scattered spinules or tubercles, and with only few short setae; dorsolateral margin distinctly delimited by row of small spines, extending nearly to tip of fixed finger (spines on dorsolateral margin larger than those on dorsal surface of palm); dorsomesial margin not delimited; lateral face with small tubercles or small, low protuberances and few short setae; mesial face with scattered spinules dorsally and low, simple, bifid or trifid protuberances or tubercles ventrally, occasionally with tufts of short setae; ventral surface convex, unarmed, but with tufts of short setae. Fixed finger with spinules at least in proximal half on dorsal surface; cutting edge with row of calcareous teeth, terminating in calcareous claw in large individuals, but in small corneous claw in small individuals. Carpus subequal in length to merus, moderately to slightly widened distally in dorsal view, maximum length 2.0 times

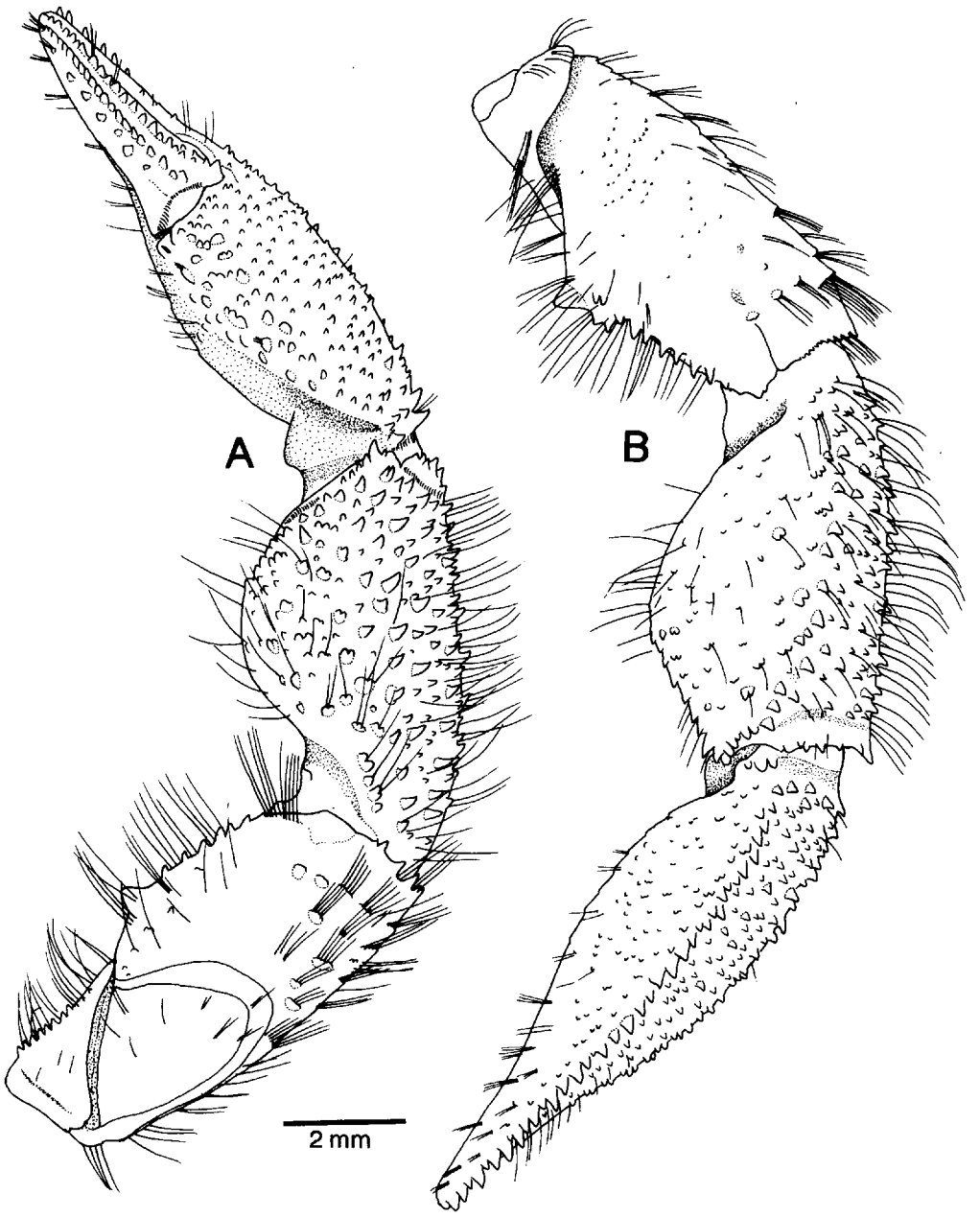

Fig. 4. *Pagurus minutus* Hess, 1865. A, right cheliped, mesial; B, same, lateral. Male (sl 6.0 mm; CBM-ZC 6473) from Kaneda Beach, Kisarazu, Tokyo Bay.

greater than distal width; dorsal surface weakly convex, covered with small spines and granules, and with numerous, but not extremely thick, moderately long setae; dorsolateral and dorsomesial margins not distinctly delimited, dorsodistal margin with row of small spines; lateral face with sparse, scattered, granules or small, low, simple or bifid protuberances, and few short setae, distal part of ventrolateral margin with row of small spines; mesial face with covering of mixture of small spines, bifid tubercles and spinules, and moderately long setae; ventral surface inflated, with several moderately long setae. Merus with several small spines on dorsodistal margin; dorsal surface with row of short, transverse, occasionally spinulose ridges each bearing moderately long setae; lateral face with few low protuberances each bearing tuft of setae and granules, ventrolateral margin with row of moderately small spines; ventral face with 1 prominent tubercle and some small tubercles and numerous long setae, ventromesial margin with row of small spines. Ischium with row of small spines and row of

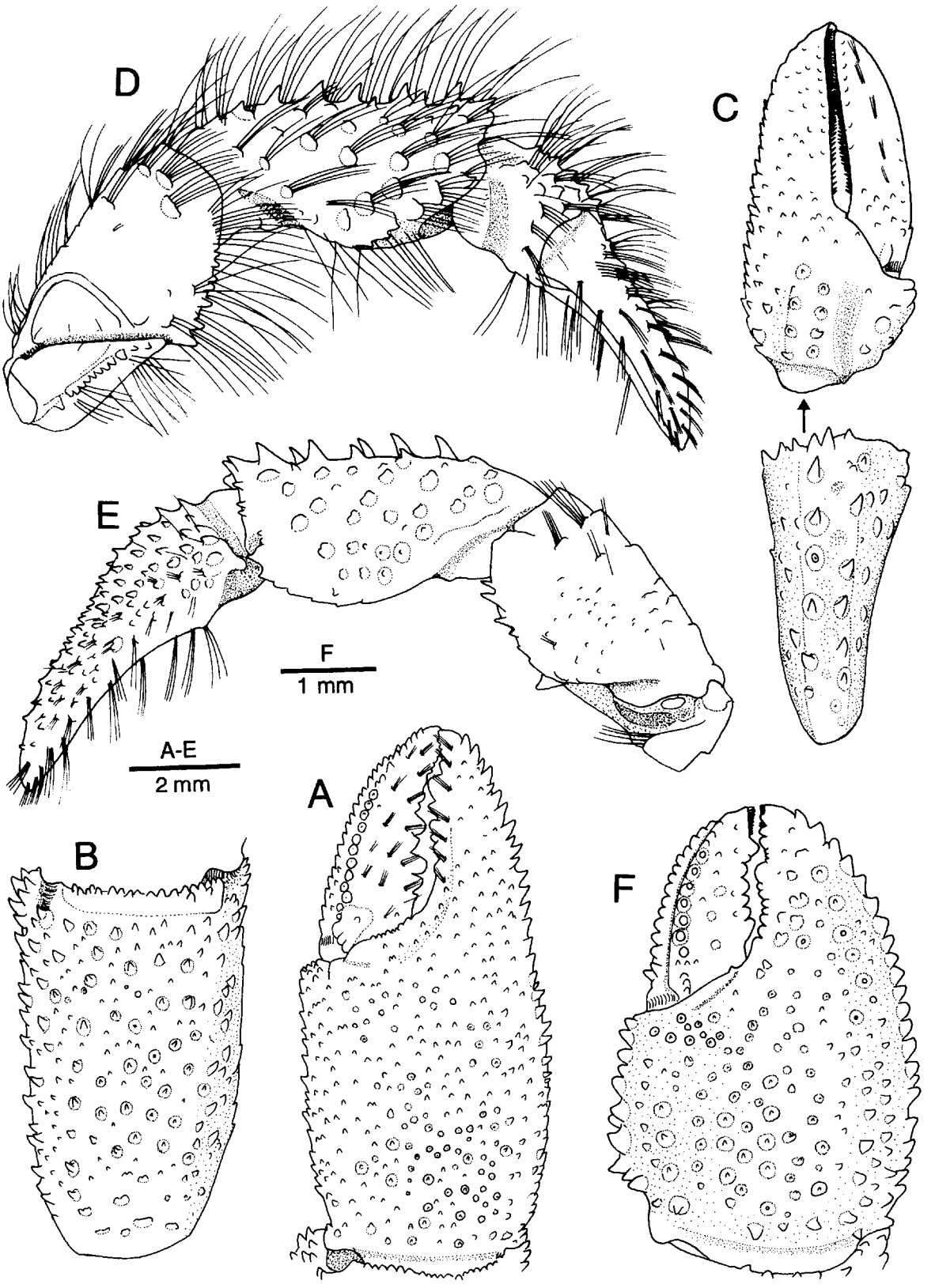

Fig. 5. *Pagurus minutus* Hess, 1865. A, F, chela of right cheliped, dorsal (setae partially omitted); B, carpus of right cheliped, dorsal (setae omitted); C, chela and carpus of left cheliped, dorsal (setae partially omitted); D, left cheliped, mesial; E, same, lateral (setae partially omitted). A-E, male (sl 6.0 mm; CBM-ZC 6473) from Kaneda Beach, Kisarazu, Tokyo Bay; F, female (sl 2.9 mm; CBM-ZC 902) from Bansho-gawa rivermouth, Saiki, Kyushu.

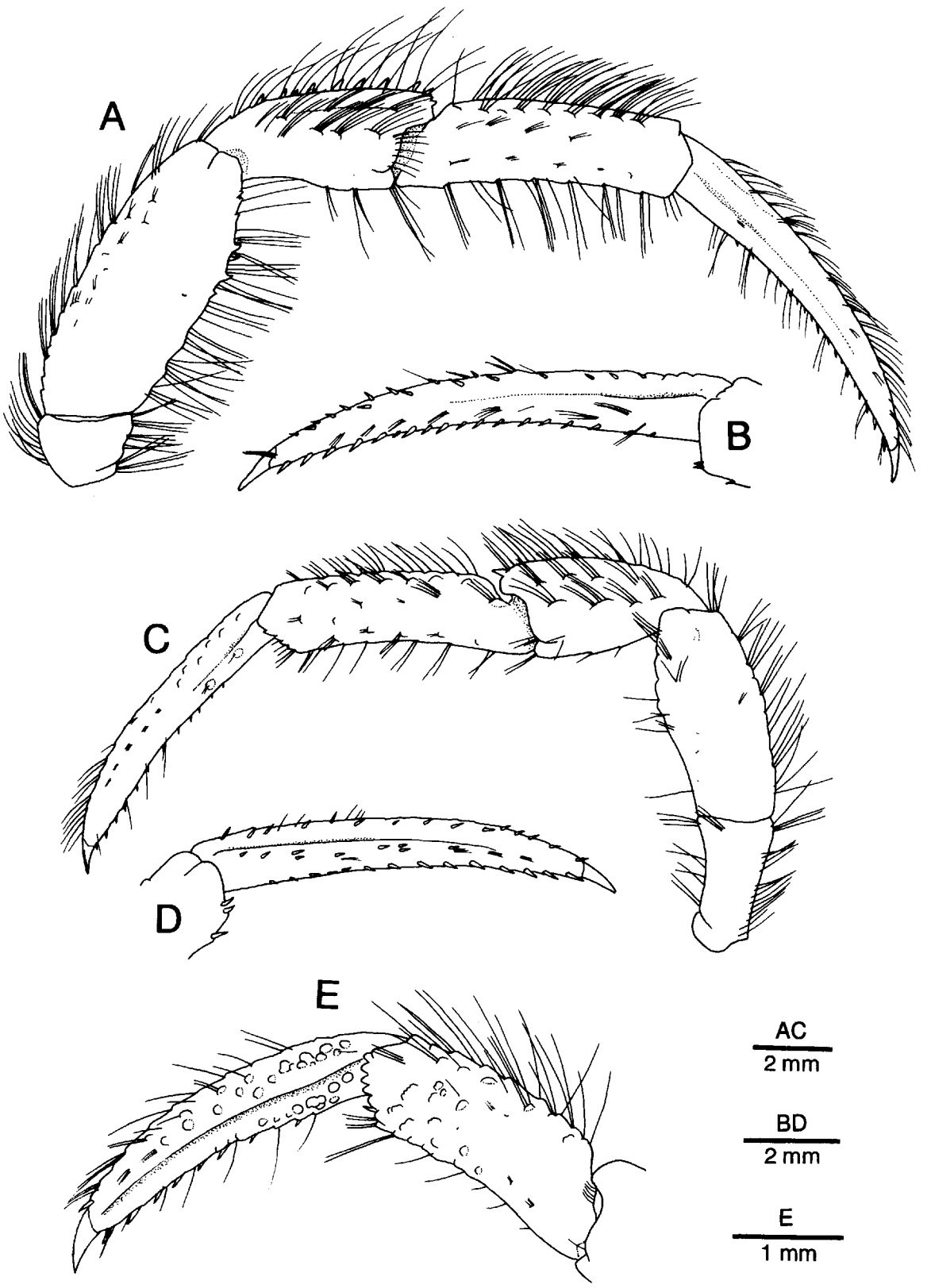

Fig. 6. *Pagurus minutus* Hess, 1865. A, right second pereopod, lateral; B, dactylus of right second pereopod, mesial (setae partially omitted); C, left third pereopod, lateral; D, dactylus of left third pereopod, mesial (setae partially omitted); E, dactylus and propodus of left third pereopod, lateral. A-D, male (sl 6.0 mm; CBM-ZC 6473) from Kaneda Beach, Kisarazu, Tokyo Bay; E, female (sl 2.9 mm; CBM-ZC 902) from Bansho-gawa rivermouth, Saiki, Kyushu.

setae on ventromesial margin; ventrolateral distal angle rounded; dorsal and lateral surfaces with tufts of setae.

Right chela of females (Fig. 5F) 1.2−1.3 times as long as wide, generally subovate in general outline in dorsal view; fingers not particularly depressed dorsoventrally. Cutting edge of dactylus with row of small corneous teeth in distal 0.2−0.3. Palm covered with numerous, scattered small spines or spinules; dorsolateral margin distinctly delimited by row of moderately small spines; dorsomesial margin also delimited by row of moderately small spines. Cutting edge of fixed finger with row of small corneous teeth interspersed by 1 or 2 small calcareous teeth on distal 0.1−0.2, terminating in small corneous claw. Carpus notably widened distally in dorsal view; dorsal surface weakly convex, covered with fewer small spines than in males; dorsomesial margin delimited by row of moderately small spines.

Left cheliped (Fig. 5C-E) reaching between midlength of palm and midlength of dactylus of right cheliped. Chela elongate subovate in general outline in dorsal view; narrow hiatus between fingers. Dactylus 2.0−2.5 times as long as palm, slightly curved ventrally; dorsal surface with some small tubercles proximally, and with rows of tufts of stiff setae, dorsomesial margin not delimited; mesial and ventral surfaces unarmed, but with rows of tufts of stiff setae; cutting edge with row of small corneous teeth over entire length, terminating in small corneous claw. Palm less than half length of carpus; dorsal surface only weakly convex, shallowly longitudinally sulcate mesiad of midline, with 2 or 3 rows of small spines occasionally extending onto fixed finger and tufts of long setae, dorsomesial surface with few small tubercles and low protuberances; dorsolateral margin weakly delimited with row of small spines decreasing in size distally on fixed finger, dorsomesial margin not delimited; lateral surface with some low protuberances proximally; mesial face with low protuberances dorsally and tufts of long setae; ventral surface slightly convex, with tufts of long setae. Fixed finger with scattered spinules on proximal half and rows of short stiff setae on distal half on dorsal surface; cutting edge with row of small corneous teeth, terminating in small corneous claw. Carpus 0.9−1.1 times as long as merus, somewhat widened distally, 1.9−2.1 times as long as distal width; dorsal surface unarmed, but weakly uneven; dorsolateral margin with row of 5−8 spines increasing in size distally and tufts of long setae; dorsomesial margin with row of 7−10 moderately large spines and tufts of long setae; dorsodistal margin laterally with row of spines decreasing in size laterally; lateral and mesial faces each with rather large, low protuberances accompanied by tufts of long setae, ventro-lateral and ventromesial margins each with row of small, subacute or blunt spines at least in distal half; ventral surface weakly convex, unarmed, but with scattered tufts of moderately long setae. Merus unarmed on dorsodistal margin; dorsal surface with some short, transverse ridges, each accompanied by long setae; lateral and mesial faces with few large, low protuberances or short, transverse ridges, each accompanied by tuft of long setae, lateral surface also with small, low tubercles, ventrolateral margin with row of small spines increasing in size distally, ventromesial margin also with row of small spines increasing in size proximally (proximalmost spine often noticeably enlarged as prominent tubercle). Ischium with row of small spines or tubercles and row of setae on ventromesial margin; ventrolateral distal angle rounded; dorsal and lateral surfaces with tufts of setae.

Second pereopods (Fig. 6A) showing tendency toward elongation in males. Dactyli slender, 1.2−1.5 times as long as propodi, slightly curved ventrally in lateral view, weakly twisted in dorsal view; dorsal surfaces slightly uneven, with stiff setae and row of corneous spinules on distal 0.3−0.5; lateral faces each with shallow longitudinal sulcus and few tufts of short setae; mesial faces (Fig. 6B) also shallowly sulcate medially, each with row of small corneous spines adjacent to dorsal margin; ventral margins each with 9−20 small corneous spines. Propodi weakly curved ventrally, with numerous tufts of moderately long setae on dorsal surface; dorsal surface unarmed; lateral faces each with dorsal row of tufts of setae and few tufts of very short setae; ventral surfaces with row of tufts of long setae and widely spaced, small corneous spines. Carpi with row of small spines on dorsal surface on right, only with dorsodistal spine on left; dorsal surfaces each with long, stiff setae; lateral faces somewhat convex, with several short, oblique rows of long setae; ventral surfaces with few tufts of long setae. Meri with numerous tufts of moderately long setae on dorsal surface; lateral faces with few short setae; ventral margins with numerous long setae and row of small spines. Ischia with numerous setae on dorsal and ventral margins.

Third pereopods of males (Fig. 6C) generally similar to second pereopods. Dactyli 1.3-1.6 times as long as propodus; dorsal surfaces each with short row of small corneous spines distally; mesial faces (Fig. 6D) each with 2 rows of small corneous spines flanking median sulcus; ventral margin with 8−20 small corneous spines. Propodi with denticulate distolateral ventral margin. Carpi only with dorsodistal spine. Meri smooth on

ventral surface.

Third pereopods of females dissimilar between right and left, right third pereopod generally similar to second pereopods. Left third pereopods relatively stouter than in males. Dactylus (Fig. 6E) strongly twisted in dorsal view; dorsal surface unarmed; lateral face strongly convex, dorsal half with several low protuberances, ventral half with low protuberances or low tubercles; mesial face with 2 rows of small corneous spines; ventral margin with 9−18 small corneous spines. Propodus (Fig. 6E) with low protuberances on dorsal surface; lateral face with several low protuberances or tubercles, particularly on ventral side; ventral surface tuberculate, occasionally terminating distally in small calcareous tooth; distolateral ventral margin denticulate. Carpus, merus, and ischium similar to those of right third pereopod. Paired gonopores present.

Fourth pereopods (Fig. 2D) moderately stout, semichelate, similar between left and right. Dactylus slightly curved, with row of small corneous teeth on ventral margin, but without preungual process. Propodus deep with strongly convex ventral margin, propodal rasp consisting of 4 or 5 rows of corneous scales. Carpus and merus with long setae on dorsal and ventral surfaces.

Fifth pereopods chelate, with paired gonopores in males, left gonopore partially obscured by tuft of setae (Fig. 2E).

Anterior lobe of sixth thoracic sternite (Fig. 2F) semicircular, skewed to left; anterior surface without denticles or spines but with numerous long setae. Eighth thoracic sternite (Fig. 2E) with 2 moderately separated anterior lobes, directed anterolaterally and somewhat produced ventrally, anterolateral margin of each lobe with dense short setae; posteromedian lobe with weakly convex surface.

Abdomen (Fig. 1) twisted, with 3 unpaired left pleopods in males, 4 unpaired left pleopods in females.

Uropods markedly unequal. Telson (Fig. 2G) with deep lateral indentations; anterior lobes with strongly convex lateral margin with row of sparse setae; posterior lobes separated by distinct median cleft, each lobe with 1−4 bristles on smooth lateral margin; terminal margins nearly horizontal to slightly oblique, each with 1 prominent spine adjacent to cleft, separated from 2 or 3 outer large spines by series of spinules.

Coloration. In life. Shield generally light yellowish brown, with dark brown median spot on gastric region and irregular markings of darker brown or grayish brown laterally. Posterior carapace generally light brown, with pair of dark brown spots just posterior to posterior margin of shield and scattered pale yellow spots on branchial regions. Ocular peduncles generally milky or yellowish white, with brown or grayish brown transverse band medially and irregular markings of grayish brown on dorsal surface. Antennular peduncles with yellowish brown ultimate segment and reddish brown penultimate segment; basal segment dark brown or black. Antennal peduncles with second and third segments generally dark brown with scattered paler spots; fourth and fifth segments generally grayish brown, former occasionally with dark brown transverse band medially; flagellum usually with 3 olive drab articles interrupted by 1 white article. Right cheliped generally dark grayish brown or olive drab (rarely reddish brown) on dorsal surface; dactylus with obscurely defined white median band and irregular brown or grayish blue patches distally and proximally on dorsal surface (except for white spines); palm usually with white median stripe extending laterally and mesially proximal to base of fixed finger; spines or tubercles on dorsal surface of palm basally grayish blue and whitish distally; ventral face of palm generally brown with white or pale grayish blue spots; carpus with spines whitish distally, lateral and mesial faces spotted by white or bluish white; merus with obscure transverse band of dark brown subdistally, lateral and mesial faces spotted by white, enlarged tubercle on ventral surface white. General color of left cheliped similar to that of right cheliped, but palm lacking white median stripe on dorsal surface. Dactyli of second and third pereopods generally dark brown or olive drab (rarely reddish brown), subdistal part whitish; lateral faces of dactyli each with longitudinally elongate white patch dorsally and occasionally ventrally, and brown or reddish brown median stripe; propodi each with dark brown median stripe on lateral face; lateral face of propodi with white or yellowish brown patch distally and proximally, remaining part around midlength grayish brown or olive drab irregularly spotted by white or grayish white; lateral face of carpi generally grayish brown or olive drab, with broad median stripe of dark brown and occasionally with obscure yellowish white patches dorsally; lateral face of meri also grayish brown or olive drab, with obscurely defined, rather irregular, transverse band of dark brown distal to level of midlength.

Variation. As is apparent from the above description, notable variation is seen in the lengthening and reduction of the armature of the right cheliped in males. The dissimilarity of the third pereopods is stronger in females than in males.

Size. Males sl 2.5−7.4 mm; females sl 2.4−5.9 mm, ovigerous females sl 2.4−5.9 mm.

Distribution. Known from temperate waters in East Asia: Japan, southern Hokkaido to Kyushu, and Okinawa Island; Primorye, Russia; Korea; northeastern coast of China; west coast of Taiwan; intertidal to 5 m.

Biological note. *Pagurus minutus* is one of the most abundant hermit crabs in temperate Japanese waters. Of the intertidal pagurid hermit crabs in the region, it is the only species commonly found on sandy or muddy flats and extending to estuarine zones. In the sand flats of the Obitsu-gawa rivermouth in Tokyo Bay, it is found in high densities in middle to high intertidal zones at least from May to September. The species also occurs occasionally on rocky shores, where the far more numerous *P. filholi* co-occurs. Kikuchi (1962, 1966) reported seasonal migration of *P. minutus* (as *Pagurus dubius*) in Tomioka Bay, Amakusa, Kyushu.

This species uses a variety of gastropod shells, such as *Chlorostoma lischkei* Tapprone-Canefri, 1874, *Monodonta labio confusa* Tapprone-Canefri, 1874, *Monodonta neritoides* (Philipi, 1849), *Umbonium costatum* (Valenciennes, 1838), *Turbo coronatus coreensis* (Récluz, 1853), *Batillaria cummingii* (Crosse, 1862), *Littorina brevicula* (Philippi, 1844), *Glossaulax didyma* (Röding, 1798), *Thais bronni* (Dunker, 1860), *Thais clavigera* (Küster, 1860), and *Rapana venosa* (Valenciennes, 1846). Local patterns of shell use may vary widely, however, depending on which shell species are locally common and perhaps also on the presence of other hermit crab species.

Affinities. *Pagurus minutus* is most similar to *P. filholi* from East Asian waters and *P. samuelis* from the northwestern coast of North America. The three species share the following characters: the right palm is covered with numerous small spines, spinules, or granules on the dorsal surface, but lacks a dense covering of tufts of setae in males; the dorsal surface of the left palm is inconspicuously elevated in the mid-line; the carpus of the second pereopod bears a row of small spines on the dorsal surface (McLaughlin 1976, Sandberg & McLaughlin 1993, Komai in press b). *Pagurus minutus* can be distinguished immediately from its two relatives by the proportionally longer dactyli of the ambulatory legs. For example, the dactylus of the left third pereopod is 1.3−1.6 times as long as the propodus in *P. minutus*, rather than 0.8−1.1 times as long in the latter three species. The less produced, rounded or bluntly triangular rostrum and the absence of a row of small calcareous spines on the ventrolateral face of the propodus of the left third pereopod in males are also useful in distinguishing *P. minutus* from *P. filholi* and *P. samuelis*. Coloration in life is quite different among the four species. *Pagurus minutus* is characteristic in having dark brown or olive drab median stripes on the lateral surfaces of the propodi and carpi of the second and third pereopods, which are absent in *P. filholi* and *P. samuelis* (personal observation; Jensen 1995).

DISCUSSION

In the original description of *Pagurus dubius* (as *Eupagurus*), Ortmann (1892) compared his new species with *Pagurus bernhardus* (Linnaeus, 1758) and *P. samuelis*. Makarov (1938, 1962) and Miyake (1978) published fairly detailed descriptions of *P. dubius*. The redescription of *P. minutus* by Sandberg & McLaughlin (1993) is detailed and accompanied by illustrations of selected parts, including the shield and cephalic appendages, chelipeds, and ambulatory legs; however, they compared *P. minutus* only with *P. filholi*, although McLaughlin (1976) had suggested a close affinity between *P. filholi* (as *P. geminus* McLaughlin, 1976) and *P. dubius*. We have now had the opportunity to examine the lectotype of *P. minutus* and the syntypes of *P. dubius*. It has been found that four of 88 specimens from Tokyo Bay (MZS 476) included in the original description of *Eupagurus dubius* actually represent a diogenid species, *Diogenes nitidimanus* Terao, 1913; therefore, a male specimen (sl 5.4 mm) (Fig. 1) is herein selected as the lectotype of *Pagurus dubius*. The lectotype of *P. minutus* and the lectotype of *P. dubius* are quite consistent in all important morphological aspects, such as the rounded or bluntly triangular rostrum, the strongly elongate right cheliped, the dorsal surface of the right palm being covered with small spinules or tubercles but lacking tufts of long setae, the possession of a prominent tubercle on the ventral surface of the merus of the right cheliped, the non-elevated mid-line of the palm of the left cheliped, the elongate dactyli of the ambulatory legs, and the lack of a row of small calcareous spines or tubercles on the ventral surface of the propodus of the left third pereopod. There is no doubt that the two taxa are conspecific. Although the name *Pagurus dubius* is far more familiar than *P. minutus* in the literature (see synonymy), the name *Pagurus minutus* has priority.

As Sandberg & McLaughlin (1993) suggested, it is probable that the type locality "Sydney" given by Hess

(1865) for *P. minutus* s.l. is inaccurate. Neither *P. filholi* nor *P. dubius* (= *P. minutus*) has ever been encountered in eastern Australian waters. Sandberg & McLaughlin (1993) noted that both of Hess' (1865) syntypes of *P. minutus*, i.e., the lectotype of *P. minutus* and the holotype of *P. filholi*, occupied shells of the gastropod *Turbo coronoatus* Gmelin, 1791. This is an intertidal gastropod species with a broad distributional range in the Indo-West Pacific (Abbott & Dance 1982). The gastropod is common in temperate waters in Japan where both *P. dubius* (= *P. minutus*) and *P. filholi* are also common (personal observation). In fact, during this study, we found that shells of a subspecies of *T. coronoatus*, *T. coronoatus coreensis*, were frequently used by *P. minutus*; therefore, it is highly probable that the types of *P. minutus* and *P. filholi* actually came from East Asian waters.

Terao (1913) placed *Eupagurus dubius* in the synonymy of *E. samuelis*, but he did not give comments.

Yokoya (1933) listed *Eupagurus dubius* from two Japanese localities, one from east of Toba in the Kumano-nada, at a depth of 91 m (*Soyo-maru*, station 370), and another from west of Tsushima, southern part of the Sea of Japan, at a depth of 120 m (*Soyo-maru*, station 461). The former specimen is still preserved in the collection of the Kitakyushu Museum of Natural History and Human History. Despite the poor condition of the specimen, it can not be referred to *Pagurus minutus* because of the following features: the corneas of the eyes are strongly dilated; the right chela is provided with a distinct row of small spines on the dorsal midline, obscured by dense setae; the propodus of the second pereopod is armed with a row of spines on the dorsal surface; and the ventral margins of the ambulatory dactyli are apparently devoid of corneous spines. Concerning the misidentification of the specimen from Kumano-nada and depth record, it seems unlikely that the other specimen from the Sea of Japan represented *P. minutus*. As mentioned before, *P. minutus* inhabits shallow water from estuarine to subtidal zone. In fact, no specimen referable to *P. minutus* collected at depths greater than 10 m has been encountered during the taxonomic study of the Paguridae in the northwestern Pacific by the senior author.

Subsequently Yokoya (1939) reported *Eupagurus dubius* from Onagawa Bay, Miyagi Prefecture, at a depth of 36 m. The identity of Yokoya's specimen remains unknown, because he did not give diagnostic information; therefore, the reference is included only questionably in the synonymy.

Makarov (1938, 1962) provided a rather detailed description of *Pagurus dubius*. Although his description generally agrees with our specimens of *P. minutus*, Makarov noted that the species generally lives at depths ranging from 50 to 120 m; in rare cases it may be found at shallower depths. However, as mentioned above, this species exclusively occurs in the intertidal and subtidal zones. It is difficult to explain this discrepancy without re-examination of the material studied by Makarov (1938, 1962).

Igarashi (1970) listed *Pagurus dubius* from Oshoro Bay (Sea of Japan) and Usujiri (Pacific coast of the Oshima Peninsula), Hokkaido. However, the published photograph (Pl. 3, fig. 10) does not depict the true *P. minutus*. Although Igarashi did not give diagnostic information on his specimens, the photograph clearly shows the dilated corneas of the eyes, the strongly inflated ventral surface of the right cheliped carpus, the absence of a prominent tubercle on the ventral surface of the right cheliped merus, the strongly elevated dorsal surface of the left palm, and the presence of dark bands on the propodi of the ambulatory legs. These features suggest that the photographed specimen most probably is *Pagurus trigonocheirus*. It is impossible to know whether Igarashi's material actually contained true *P. minutus* without reexamination of the entire lot.

Yu & Foo (1990) reported *P. dubius* from Taiwan. However, the figured specimen does not agree with *P. minutus*, the former having shorter ambulatory dactyli and different coloration. Examination of specimens from the northeastern part of Taiwan that agree with the specimen reported by Yu & Foo (1990) has shown that they represent an undescribed species of *Pagurus*. The occurrence of *P. minutus* in Taiwan was confirmed by the examination of the two specimens from the western coast deposited in the collection of NTOU.

The color photograph provided by Matsukubo (1999) does not depict the true *P. dubius*, but an undescribed species previously assigned to *P. pilosipes* s.l. (see Komai, in press b).

Minemizu (2000) presented a color photograph of *P. dubius* from the Izu Peninsula. The numerous long setae on the right palm and the two brown bands on respective propodus of the ambulatory legs are clearly depicted. Thus, the figured specimen can not be referred to *P. minutus*, but most certainly belongs to *P. proximus*.

Davie (2002) included *Pagurus minutus* in his catalogue of the decapod crustaceans of Australia in reference to Hess' (1865) original indication of the type locality for the species, although he mentioned that the species might not be part of the Australian fauna, citing Sandberg and McLaughlin (1993).

Komai (in press a) has shown that the two specimens from Yokohama, Tokyo Bay, referred to *Eupagurus similis* by Doflein (1902) actually represent *P. minutus* (as *P. dubius*).

The nomenclatural confusion regarding the two species described by Benedict (1892) as *Eupagurus minutus* and *E. munitus* was discussed by McLaughlin (1974) and Sandberg & McLaughlin (1993).

Acknowledgments. We sincerely thank E. Lang and curatorial staff of the Musee Zoologique, Strasbourg, for generous help and warm hospitality during the senior author's stays in 1997 and 1998, and K. Sindemark of the Swedish Museum of Natural History for sending us the lectotype of *Pagurus minutus* on loan. Thanks are extended to the following scientists for making specimens available for this study: T.-Y. Chan of the Institute of Marine Biology, National Taiwan Ocean University; F. Muto of the Faculty of Fisheries, Hokkaido University; and K. Nomura of the Kushimoto Marine Park. We also thank M. Osawa of the National Science Museum, Tokyo, for providing us with copies of some literature and for reviewing the manuscript, and for P. A. McLaughlin for reviewing the manuscript and offering a number of suggestions for improvement.

REFERENCES

Abbott, T. and S. P. Dance 1982. *Conpendium of Seashells.* E. P. Dutton, Inc., New York, 443 pp.

Alcock, A. 1905. Anomura. Fascicule I. Pagurides. *Catalogue of the Indian Decapod Crustacea in the Collections of the Indian Museum,* 2. Indian Museum, Calcutta, xi+197 pp., pls. 1-16.

Asakura, A. 1995. Anomura. In, *Guide to Sea Shore Animals of Japan with Color Pictures and Keys,* Volume II, Nishimura, S. (ed.), Hoikusha, Osaka, pp. 347-378, pls. 93-100 (in Japanese).

Balss, H. 1913. Ostasiatische Decapoden, I. Die Galatheidae und Paguridae. Beiträge zur Naturgeschichte Ostasiens, herausgegeben von Pr. F. Doflein. *Abhandlungen der Königlichen Bayerischen Akademie der Wissenschaften, Mathematisch-physikalische Klasse,* Supplement 2: 1-85, pls. 1, 2.

Benedict, J. 1892. Preliminary descriptions of thirty-seven new species of hermit crabs of the genus *Eupagurus* in the U.S. National Museum. *Proceedings of the U.S. National Museum,* 15: 1-36.

Davie, P. J. F. 2002. *Crustacea: Malacostraca: Eucarida (Part 2): Decapoda Anomura, Brachyura. Zoological Catalogue of Australia,* Vol. 19.3B, Wells, A. and W. W. K. Houston (eds.), CSIRO Publishing, Melbourne, xiv+641 pp.

Derjugin, K. M. and Z. I. Kobjakova 1935. Zur Dekapodenfauna des japanischen Meeres. *Zoologischer Anzeiger,* 112: 141-147.

Doflein, F. 1902. Ostasiatische Dekapoden. *Abhandlungen der Königlich Bayerischen Akademie der Wissenschaften, mathematisch-physikalishe Klasse,* 21: 613-679, pls 1-6.

Fabricius, J. C. 1775. *Systema Entomologiae, sistens Insectorum Classes, Ordines, Genera, Species, Adjectis, Synonymis, Locis, Descriptionibus, Observationibus.* Officina Libraria Kortii, Flensburgi et Lipsiae, 832 pp.

Gordan, J. 1956. A bibliography of pagurid crabs, exclusive of Alcock, 1905. *Bulletin of the American Museum of Natural History,* 108: 253-352.

Haswell, W. A. 1882. *Catalogue of the Australian Stalk-eyed Crustacea.* Australian Museum, Sydney, xxiv+326 pp., 4 pls.

Hess, W. 1865. Beiträge zur Kenntnis der Decapoden-Krebse Ost-Australiens. *Archiv für Naturgeschchte,* 31: 127-173, pls. 6, 7. [also printed separately - *Beiträge zur Kenntnis der Decapoden-Krebse Ost-Australiens.* Bonn, 47 pp., pls. 6, 7].

Igarashi, T. 1970. A list of marine decapod crustaceans from Hokkaido, deposited at the Fisheries Museum, Faculty of Fisheries, Hokkaido University II. Anomura. *Contributions from the Fisheries Museum, Faculty of Fisheries, Hokkaido University,* 12: 1-15, pls. 1-9.

Jensen, G. C. 1995. *Pacific Coast Crabs and Shrimps.* Sea Challengers, Monterey, California, viii+87 pp.

Kikuchi, T. 1962. An ecological study on animal community of *Zostera* belt in Tomioka Bay, Amakusa, Kyushu (II). Community composition (2). Decapod crustaceans. *Records of Oceanographic Works in Japan,* Special No. 6: 135-146.

Kikuchi, T. 1966. An ecological study on animal communities of the *Zostera marina* belt in Tomioka Bay, Amakusa, Kyushu. *Publication of the Amakusa Marine Biological Laboratory, Kyushu University,* 1: 1-106.

Kim, H. S. 1963. On the distribution of anomuran decapods of Korea. *Journal of Sung Kyun Kwan University,* 8: 287-311 (in Korean).

Kim, H. S. 1964. A study on the geographical distribution of anomuran decapods of Korea, with consideration of its oceanographic conditions. *Journal of Sung Kyun Kwan University,* 8 (Supplement): 1-15, pl. 1 (in Korean).

Kim, H. S. 1970. A check list of the Anomura and Brachyura (Crustacea, Decapoda) of Korea. *Journal of Seoul National University, Biology and Agriculture,* series B, 21: 1-29, pls. 1-5.

Kim, H. S. 1973. *Illustrated Encyclopedia of Fauna and Flora of Korea, Volume 14. Anomura and Brachyura.* Samhwa Publishing Co., Seoul, 694 pp., 112 pls. (in Korean).

Kobjakova, Z. I. 1967. Systematic review (Crustacea

Decapoda) of Possjet Bay (Sea of Japan). *Issledovanija Fauny Morei SSSR,* 5: 236-247 (in Russian).

Komai, T. In press a. Identities of *Pagurus japonicus* (Stimpson) and *P. similis* (Ortmann), with description of a new species heretofore assigned to *P. similis* (Decapoda, Anomura, Paguridae). *Zoosystema.*

Komai, T. In press b. 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). *Natural History Research,* 7.

Komai, T. and M. Osawa 2001. A new distinctive species of pagurid hermit crab (Crustacea: Decapoda: Anomura) from Japan. *Zoological Science,* 18: 1291-1301.

Komai, T., S. Maruyama and K. Konishi 1992. A list of decapod Crustacea from Hokkaido, northern Japan. *Researches on Crustacea,* 21: 189-205 (in Japanese with English abstract).

Lemaitre, R. 1995. A review of the hermit crabs of the genus *Xylopagurus* A. Milne Edwards, 1880 (Crustacea: Decapoda: Paguridae), including descriptions of two new species. *Smithsonian Contributions to Zoology,* 570: 1-27.

Matsukubo, K. 1999. *Seashore Creatures of Japan. Field Guide Volume 20.* Shogaku-kan, Tokyo, 300 pp. (in Japanese).

Makarov, V. V. 1938. *Rakoobraznyey. Anomura. [Crustacés Décapodes Anomures]. Fauna SSSR 10.* Akademii Nauk SSSR, Moscow and Leningrad, x+396 pp., 5 pls. (in Russian with English summary).

Makarov, V. V. 1962. *Crustacea. Anomura. Fauna of U.S.S.R. 10.* Translated from Russian by the Israel Program for Scientific Translations, Jerusalem, 278 pp., 5 pls.

Man, J. G. de. 1887. Übersicht der indo-pacifischen Arten der Gattung *Sesarma* Say, nebst einer Kritik der von W. Hess und E. Nauck in den Jahren 1865 und 1880 beschriebenen Decapoden. *Zoologische Jahrbücher, Abtheilung fur Systematik, Geographie und Biologie der Thiere,* 2: 639-722, pl. 17.

McLaughlin, P. A. 1974. The hermit crabs (Crustacea Decapoda, Paguridea) of northwestern North America. *Zoologische Verhandelingen,* 130: 1-396, pl. 1.

McLaughlin, P. A. 1976. A new Japanese hermit crab (Decapoda, Paguridae) resembling *Pagurus samuelis* (Stimpson). *Crustaceana,* 30: 13-26.

McLaughlin, P. A. 1997. Crustacea Decapoda: Hermit crabs of the family Paguridae from the KARUBAR Cruise in Indonesia. In, *Résultats des Campagnes MUSORSTOM, Volume 16,* Crosnier, A. (ed.). *Mémoires du Muséum National d'Histoire Naturelle,* 172: 433-572.

McLaughlin, P. A. and M. de Saint Laurent 1998. A new genus for four species of hermit crabs heretofore assigned to the genus *Pagurus* Fabricius (Decapoda: Anomura: Paguridae). *Proceedings of the Biological Society of Washington,* 111: 158-187.

Minei, H. 1973. Studies on the hermit crabs (Anomura, Paguridae) of the Ryukyu Islands. *Biological Magazine Okinawa,* 10: 43-56 (in Japanese).

Minemizu, R. 2000. *Marine Decapod and Stomatopod Crustaceans Mainly from Japan.* Bun'ichi Sogo Publishing Co., Tokyo, 344 pp. (in Japanese).

Miyake, S. 1957. Anomuran decapod fauna of Hokkaido, Japan. *Journal of the Faculty of Science, Hokkaido University,* Series 6, 13: 85-92.

Miyake, S. 1960. Anomura. In, *Encyclopedia Zoologica Illustrated in Colours,* Hokuryu-kan, Tokyo, pp. 89-97, pls. 44-48 (in Japanese).

Miyake, S. 1961a. *Decapod Crustacea. Fauna and Flora of the Sea around the Amakusa Marine Biological Laboratory, 2.* Amakusa Marine Biological Laboratory, Kyushu University, Amakusa, 30 pp. (in Japanese).

Miyake, S. 1961b. A list of the decapod Crustacea of the Sea of Ariaké, Kyushu. *Records of Oceanographic Works in Japan,* Special No. 5: 165-178.

Miyake, S. 1965. Anomura. In, *New Illustrated Encyclopedia of the Fauna of Japan,* Okada, K., S. Uchida and T. Uchida (eds.), Hokuryu-kan, Tokyo, pp. 630-652 (in Japanese).

Miyake, S. 1975. Anomura. In, *Freshwater and Marine Animals,* Utinomi, F. (ed.), Gakushu-kenkyu-sha, Tokyo, pp. 110-119, 187-1115 (in Japanese).

Miyake, S. 1978. *The Crustacean Anomura of Sagami Bay.* Biological Laboratory, Imperial Household, Tokyo, ix+200 pp. (in English), 161 pp. (in Japanese).

Miyake, S. 1982. *Japanese Crustacean Decapods and Stomatopods in Color, Volume 1: Macrura, Anomura and Stomatopoda.* Hoikusha, Osaka, viii+261 pp., 56 pls. (in Japanese).

Miyake, S. 1991. *Japanese Crustacean Decapods and Stomatopods in Color, Volume 1: Macrura, Anomura and Stomatopoda.* Second printing. Hoikusha, Osaka, viii+261 pp., 56 pls. (in Japanese).

Miyake, S. 1998. *Japanese Crustacean Decapods and Stomatopods in Color, Volume 1: Macrura, Anomura and Stomatopoda.* Third printing. Hoikusha, Osaka, viii+261 pp., 56 pls. (in Japanese).

Miyake, S. and M. Imafuku 1980. Hermit crabs from Kii Peninsula, II. *Nankiseibutu,* 22: 59-64 (in Japanese).

Miyake S., K. Sakai and S. Nishikawa 1962. A fauna list of the decapod Crustacea from the coasts washed by the Tsushima warm current. *Records of the Oceanographic Works in Japan,* 6: 121-131.

Ortmann, A. 1892. Die Decapoden-Krebse des Strassburger Museums, mit besonderer Berücksichtigung der von Herrn

Dr. Döderlein bei Japan und bei den Liu-Kiu-Inseln gesammelten und zur Zeit im Strassburger Museum aufbewahrten Formen, IV. Die Abtheilungen Galatheidea und Paguridea. *Zoologischen Jahrbücher, Abtheilung fur Systematik, Geographie und Biologie der Thiere,* 6: 241-326, pls. 11-12.

Sandberg, L. and P. A. McLaughlin 1993. Reexamination of *Pagurus minutus* Hess, 1865, and *Pagurus filholi* (de Man, 1887) (Crustacea: Anomura: Paguridae). *Zoologische Mededelingen, Leiden,* 67: 197-206.

Suzuki, K. 1971. Decapod Crustaceans. In, *Common Sea Shore Animals of Japan in Color,* Nishimura, S. and K. Suzuki (eds.), Hoikusha, Osaka, 77-125, pls. 26-46 (in Japanese).

Takeda, M. 1982. *Keys to the Japanese and Foreign Crustaceans Fully Illustrated in Colors.* Hokuryukan, Tokyo. vi+58 pp. (keys), 284 pp. (text and illustrations) (in Japanese).

Terao, A. 1913. A catalogue of hermit-crabs found in Japan (Paguridae excluding Lithodidae), with descriptions of four new species. *Annotationes Zoologicae Japonenses,* 8: 355-391.

Vinogradov, L. G. 1950. A key to the shrimps, lobsters, and crabs of the Far East. *Izvestija Tikhookeanskogo Nauchno-Issledovaniskogo Instituta Rybnogo Khozjaistva i Okeanografii,* 33: 179-358, pls. 1-53 (in Russian).

Wang, F.-Z. 1994. Anomura. In, *Marine Species and their Distributions in China's Seas,* Huang, Z-G. (ed.), China Ocean Press, Beijing, pp. 568-576 (in Chinese).

Yokoya, Y. 1933. On the distribution of decapod Crustacea inhabiting the continental shelf around Japan, chiefly based upon the materials collected by S.S. "Soyo Maru" during the years 1923-1930. *Journal of the College of Agriculture, Tokyo Imperial University,* 12: 1-236.

Yokoya, Y. 1939. Macrura and Anomura of decapod Crustacea found in the neighbourhood of Onagawa, Miyagi-ken. *Science Reports of Tohoku Imperial University,* 14: 261-289.

Yu, H.-P. and K.-Y. Foo 1990. *Hermit Crabs of Taiwan. SMC Color Series 8.* SMC Publishing Inc., Taipei, 78 pp. (in Chinese).