# HEMIGRAPSUS TAKANOI, NEW SPECIES, A SIBLING SPECIES OF THE COMMON JAPANESE INTERTIDAL CRAB H. PENICILLATUS (DECAPODA: BRACHYURA: GRAPSOIDEA)

### Akira Asakura and Seiichi Watanabe

(AA, correspondence) Natural History Museum and Institute, Chiba, 955-2, Aoba-cho, Chuo-ku, Chiba 260-8682, Japan (asakura@chiba-muse.or.jp); (SW) Department of Marine Bioscience, Faculty of Marine Science, Tokyo University of Marine Science and Technology, 4-5-7, Konan, Minato-ku, 108-8477, Japan

### ABSTRACT

The two forms of *Hemigrapsus penicillatus* (de Haan, 1835), recently distinguished on the basis of electrophoresis and differences in the size of the setal patches on the male chelae, are here recognized as two distinct species. The individuals having smaller setal patches are *H. penicillatus*, whereas those with larger setal patches are described herein as a new species. Living and fresh material of the two species are also clearly separated by the size and distribution of dark spots on the cephalothorax, abdomen, third maxillipeds, and chelipeds. Morphology of the male first pleopod is different between the two species. Females of the two species are morphologically identical and cannot be easily separated once colour has faded.

The small grapsoid crab *Hemigrapsus penicillatus* (de Haan, 1835) is known from Japan (Sakhalin Island, Hokkaido to Kagoshima, Okinawa) and the adjacent waters of Taiwan, Korea, and China (e.g., Sakai, 1976, Miyake, 1983, Fukui et al., 1989). There is also an unconfirmed record from Hawaii by Edmondson (1959). It is common under boulders in intertidal areas of estuaries, lagoons, boulder beaches, and wave-sheltered rocky shores. A recent electrophoretic study by Takano et al. (1997) found two genetically isolated populations with fixed differences at three enzyme loci (6Pgd: 6-Phosphoglucomutase, Aat-2: Aspartate aminotransferase, and Pgm: Phosphoglucomutase). Individuals of one population possess alleles  $6Pgd^B$ , Aat-2C, and  $Pgm^A$ , while those of the other have  $6Pgd^C$ , Aat-2B, and  $Pgm^B$ . Takano *et al.* (1997) referred to the former as form I and the latter as form II. Heterozygote individuals (genotype B/C) were not observed at the 6Pgd locus.

Takano *et al.* (1997) also found that individuals of form II had statistically significantly larger sized setal patches on the male chelae than those of form I. They concluded that the two forms represented sibling species (sets of species difficult to distinguish using traditional morphological characters, but which are reproductively isolated (Mayr, 1963, see also Knowlton, 1986, 1993 for examples of decapod crustaceans)). The two forms occur sympatrically in temperate Japanese waters, including Honshu, Shikoku, and Kyushu (Takano *et al.*, 1999).

A recent intensive ecological study of *H. penicillatus* by the second author (SW) and Satoshi Akiwa clarified differences in spatial distribution of the two forms in Tokyo Bay. They investigated 18 localities along the west and east coasts of the bay and collected 607 individuals of form I and 916 of form II. Although both forms were very common and occurred sympatrically in most localities, form II was mainly distributed on the inner side of Tokyo Bay, while form I was more abundant toward the mouth of the Bay (Watanabe and Akiwa, unpublished data).

They also found that the two forms differ in their colour patterns: form I has large dark spots on the ventral surface of the cephalothorax, on the ocular peduncles, on the third maxillipeds, and on the abdominal segments, as well as on the outer faces of the chelipeds. On form II, the dark spots do not occur on the abdominal segments, and the dark spots are comparatively smaller (Watanabe and Akiwa, unpublished data).

Furthermore, Winda Mercedes Mingkid, a graduate course student of the second author (SW), examined over 200 males of each form and found morphological differences in the first pleopods between the two (Mingkid, unpublished data).

Finally, Watanabe (2003) recognized a statistically significant difference in the volume of eggs carried by females of the two forms, with a mean egg volume of 0.0103 mm<sup>3</sup> in form I and 0.0141 mm<sup>3</sup> in form II.

The combined evidence from electrophoresis, morphology (including colour pattern), and ecology, clearly indicates that the two forms must represent separate species.

The type series of H. penicillatus was deposited in Rijksmuseum van Natuurlijke Histoire, Leiden (now Nationaal Natuurhistorisch Museum, Leiden) (RMNH). Subsequently, a small part of this series was transferred to the Museum national d'Histoire naturelle, Paris (MNHN) (Yamaguchi, 1993). Following an investigation of the Siebold collection in the RMNH and crustacean collections in other European museums by Takao Yamaguchi of Kumamoto University and his coworkers, Yamaguchi and Baba (1993) selected a lectotype for *H. penicillatus*, a male collected from Japan during 1823-1829 by von Siebold (RMNH D200). Nine other males, five females, and eight sex indeterminate juveniles (RMNH D164, 201, 203, D42130, D42131, D45224, MNHN-B 3506, MNHN-B 11012, MNHN-B 12837) are paralectotypes (Yamaguchi and Baba, 2003). The collection localities are all indicated only as "Japan." As discussed later, the types series is mixed

and contains specimens of both *H. penicillatus* and its closely related new species described herein.

Dr. C. H. J. M. Fransen (RMNH) kindly sketched the outer face of the chela of the lectotype (see Fig. 9B). It is clearly conspecific with form I of Takano *et al.* (1997). Accordingly, their form II is herein described as a new species, *Hemigrapsus takanoi*.

Measurements provided are of carapace width and length in mm respectively. The material recently collected from Tokyo Bay during the ecological study by the second author and his students have been used as part of the study, and have been deposited at the Natural History Museum and Institute, Chiba (CBM-ZC). We also examined material collected from various localities in Japan, housed in the Osaka Museum of Natural History (OMNH) and Toyama Science Museum (TOYA), as well as material recently collected from Hokkaido and Tohoku, Japan. Further, the material recently collected from European waters (apparently introduced by accident) that is housed in the Natural History Museum, London (NHM) was also examined. For locality data, the following abbreviations are used; PACIFIC: Pacific coast of Japan; SEA-JAPAN: coast of the Sea of Japan; SETO: coast of Seto Inland Sea; HKK: Hokkaido Island; HON: Honshu Island; SHI: Shikoku Island; KYU: Kyushu Island.

#### Systematics

# *Hemigrapsus takanoi*, new species Figs. 1–5, 6A–C, 7

Grapsus (Eriocheir) penicillatus de Haan, 1835: 60, pl. 11, fig. 5. (in part). Brachynotus penicillatus.—Miers, 1886: 264 (in part?).—Tesch, 1918: 104 (in part?).—Balss, 1922: 150 (in part?).

Heterograpsus penicillatus.—Ortmann, 1894: 714 (in part?).—Parisi, 1918: 101 (in part?).

Hemigrapsus peniciliatus.—Stimpson, 1907: 126 (on foot-note) (in part?).—Shen, 1932: 163, text-figs. 104, 105, pl. 7, fig. 2 (in part?).—Sakai, 1939: 673 (in part?), pl. 75, fig. 1.—Kamita, 1941: 204, text-figs. 113a, b (in part?).—Sakai, 1957: 82, pl. 41.— Miyake, 1961: 176 (list).—Miyake et al., 1962: 130 (list) (in part?).—Sakai, 1965: 198 (in part?), pl. 94, fig. 3.—Nishimura and Suzuki, 1971: pl. 45-4, 124 (in part?).—Takeda: 1975, 146 (unnumbered photo).—Sakai, 1976: 650 (English Part) (in part?), 403 (Japanese Part) (in part?), pl. 222, fig. 2.—Kikuchi and Miyake, 1978: 44 (list) (in part?).—Tsutsumi and Takemura, 1980: 137.— Sakai, 1982: 717 (?).—Takeda, 1982: 218, fig. 647.—Miyake, 1983: 175 (in part?), pl. 59-4.—Sakai and Nakano, 1983: 88 (in part?).—Aiyun and Siliang, 1986: 478 (key), 478, figs. 269-2, 269-3, pl. 67-5 (in part?).—Nishimura and Ito, 1987: 123 (unnumbered photo), 124 (?).—Yamaguchi et al., 1987: 31, pl. 15, fig. 2a, 2b (in part?).—Inaba, 1988: 107 (in part?).—Takeda and Hayashi, 1990: 56 (?).—Fukui et al., 1989: 229, 236 (list) (?).—Aiyun and Siliang, 1991: 524 (key), 525, figs. 269-2, 269-3, pl. 67-5 (in part?).— Yamaguchi and Baba, 1993: 178, figs. 178A, 178-B, 178-C (in part).—Wada, 1995: pl. 114, fig. 7, 408 (in part?).—Takeda and Kawashima, 1997: 216.—Noël et al., 1997: 741.—Muraoka, 1998: 53 (in part?).—Breton et al., 2002: 187, fig. 2B.—d'Udekem d'Acoz and Faasse, 2002: 107, figs. 2B, 3B, 4.

Brachynotus brevidigitalis.—Yokoya, 1928: 780, text-fig 8 (in part?).
?Hemigrapsus penicillatus.—Edmondson, 1959: 180, fig. 14.
Hemigrapsus sanguineus.—Nishimura and Suzuki, 1971: pl. 45-3. [not Hemigrapsus sanguineus (de Haan).]

*Material Examined.*—Holotype:  $\circlearrowleft$ , 21.3  $\times$  18.4, intertidal, estuary of Okamoto-gawa, Tomiura, Chiba Pref., Boso Peninsula, east coast of Tokyo Bay, HON, PACIFIC, 9 Aug. 2002, coll. Satoshi Akiwa, CBM-ZC 8039. Paratypes:  $1 \circlearrowleft$ , 22.5  $\times$  19.8, intertidal, Kasai Rinkai Park, Edogawaku-ku, Tokyo, innermost of Tokyo Bay, HON, PACIFIC, 9 Mar. 2004, coll. Winda Mercedes Mingkid, CBM-ZC 8119;  $10 \circlearrowleft$ ,  $16.7 \times 12.9$ – $23.9 \times 21.2$ ,

10<sup>♀</sup>, 16.3 × 9.9–23.0 × 20.2, intertidal, Oui-futo Kaihin-kouen, (= Oui Wharf Seaside Park), Shinagawa-ku, Tokyo, innermost of Tokyo Bay, HON, PACIFIC, 2 May 2002, coll. Satoshi Akiwa, CBM-ZC 8040; 175,  $10.2 \times 9.2 - 21.4 \times 19.3$ ,  $15^{\circ}_{+}$ ,  $10.4 \times 9.5 - 15.2 \times 13.8$ , intertidal, Sanban-ze, off Funabashi Kaihin Park, Chiba Pref., innermost of Tokyo Bay, HON, PACIFIC, 22 Aug. 2002, coll. Satoshi Akiwa, CBM-ZC 8041; 43, 16.9 ×  $15.3-19.2 \times 16.9$ , 12,  $18.0 \times 16.0$ , intertidal, Ena Bay, Miura Peninsula, Kanagawa Pref., west coast of Tokyo Bay, HON, PACIFIC, 25 July 2002, coll. Satoshi Akiwa, CBM-ZC 8042; 12♂, 11.2×9.5–19.7×17.4, 6♀, 10.6  $\times$  9.9–16.2  $\times$  14.0, intertidal, mouth of Tsurumi river, under Tsurumi Ohashi Bridge, Yokohama-shi, Kanagawa Pref., innermost of Tokyo Bay, HON, PACIFIC, 26 Aug. 2002, coll. Satoshi Akiwa, CBM-ZC 8043; 10%,  $8.1 \times 12.2 - 24.5 \times 20.3$ , 10,  $15.5 \times 13.6 - 23.5 \times 20.7$ , intertidal, Kattoshimisaki, Hakodate Bay, HKK, Tsugaru Strait, 41°44'22"N, 140°36'11"E, Aug. 2004, coll. T. Oba and S. Goshima, CBM-ZC 8044; 145, 8.7 × 7.8- $27.2 \times 23.3$ , 9,  $17.5 \times 15.7$ – $21.6 \times 19.1$ , river mouth, Oritate-gawa River, under boulders, Shizugawa-cho, Motoyoshi-gun, Miyagi Pref., HON, PACIFIC, 20 July 2004, coll. K. Tanaka, CBM ZC-8045. Nontype material: 33,  $21.3 \times 19.0-24.6 \times 30.9$ ,  $2^{\circ}_{+}$ ,  $7.9 \times 11.7-31.3 \times 28$ , Kakijima, Akkeshi-machi, HKK, PACIFIC, 1 July 1980, coll. R. Yamanishi, OMNH Ar 2354 (Z80-56); 13, 24.4 × 22.1, Aikappu, Akkeshi-machi, HKK, PACIFIC, 30 June 1980, coll. R. Yamanishi, OMNH Ar 2351 (Z80-55); 23, 12.8 × 11.5–21.3 × 18.6, Akahama, Ootsuchi-machi, Kamiheigun, Iwate Pref., HON, PACIFIC, 4 Aug. 1993, coll. N. Nunomura, TOYA Cr 13055–13056 (Z93-25); 13, 17.8  $\times$  15.2, 12, 16.4  $\times$  14.7, intertidal, Ena Bay, Miura-shi, Miura Peninsula, Kanagawa Pref., HON, PACIFIC, June 2001, coll., H. Ikeda, HSM-crb-599; 1♂, 11.2 × 9.7, Higashihanzu, Hanzucho, Hanzu-gun, Aichi Pref., HON, PACIFIC, 15 Dec. 1989, coll. H. Nanbu, TOYA Cr 8934–8937; 13, 14.3  $\times$  12.3, 1 $\updownarrow$ , 10.7  $\times$  9.0, Hanzu-cho, Hanzu-gun, Aichi Pref., HON, PACIFIC, 15 Dec. 1989, coll. H. Nanbu, TOYA Cr-13057–13058 (Z89-31); 43,  $12.1 \times 10.5 - 20.6 \times 17.5$ , 49,  $6.5 \times 10.5 + 10.5 = 10.5$ 5.9-16.9 × 14.7, Miyazaki, Asahi-machi, Shimoniikawa-gun, Toyama Pref., HON, SEA-JAPAN, 2 Sept. 1982, coll. N. Nunomura, TOYA Cr-13060–13067 Z82-44; 2♂, 13.4 × 11.7–16.9 × 15.1, Aio Harbor, Aio-cho, Yoshiki-gun, Yamaguchi Pref., HON, SETO, 24 May 1994, coll. R. Yamanishi, OMNH Ar 4503 (Z00-33); 2♂, 21.1 × 18.4–21.3 × 18.8, 1♀, 18.9 × 16.8, Ooshimano-hana, Yokonami, Susaki-shi, Kochi Pref., SHI, PACIFIC, 29 May 1980, coll. R. Yamanishi, OMNH Ar 2354; 23, 22.7  $\times$ 20.0-32.5 × 27.3, river mouth, Takori-gawa River, Tara-machi, Fujitsugun, Saga Pref., KYU, SEA-JAPAN, coll. Osaka-wan Kaigan-seibutsu Kenkyukai (= Research Club of Marine Organisms in Osaka Bay), 15 May 1999, OMNH Ar 4280; 63,  $11.5 \times 10.4 - 18.2 \times 16.2$ , river mouth, Midorikawa River, Sumiyoshi, Kumamoto Pref., KYU, SEA-JAPAN, coll. Osakawan Kaigan-seibutsu Kenkyukai (= Research Club of Marine Organisms in Osaka Bay), 17 May 1999, OMNH Ar 4342 (Z99-42); 23, 20.8 × 18-24.3 × 20.4, Aitsu, Matushima-machi, Amakusa-gun, Kumamoto Pref., KYU, SEA-JAPAN, 17 May 1991 coll. N. Nunomura, TOYA Cr-13068-13069 (Z91-8) 13, 19.2 × 16.8, 12, 18.0 × 16.1, intertidal zone, Talmont, estuary of La Gironde (Charente-maritime, France), 45°32'N, 00°54'W, 9 May 1996, coll. P. Noël, NHM 1997: 2-3.

Description.—Carapace (Fig. 1) subquadrate; greatest width between second anterolateral teeth, 1.10–1.20 times broader than long; slightly vaulted. Surface naked, minutely granulated, particularly anteriorly; gastric and cardiac regions separated by H-shaped groove. Front about half greatest carapace breadth, slightly deflexed downwards, anterior margin slightly concave medially. Supraorbital margin sinuous, entire. Exorbital tooth distinct; 3 anterolateral teeth, third smallest. Posterolateral margin slightly concave, weakly converging posteriorly. Infraorbital ridge (Fig. 2B) composed of long inner ridge armed with tubercles or granules, short, swollen middle ridge, and outer very short ridge.

Third maxillipeds (Fig. 2A) each with ischium bearing distinct sulcus; exopod slender.

Male chelipeds (Fig. 3) subequal, large and robust, generally smooth. Merus with chitinous crest near ventral margin of inner face (Fig. 3E). Carpus generally smooth. Palm generally smooth except for indistinct row of protuberances on proximal half of inner surface, and long longitudinal row

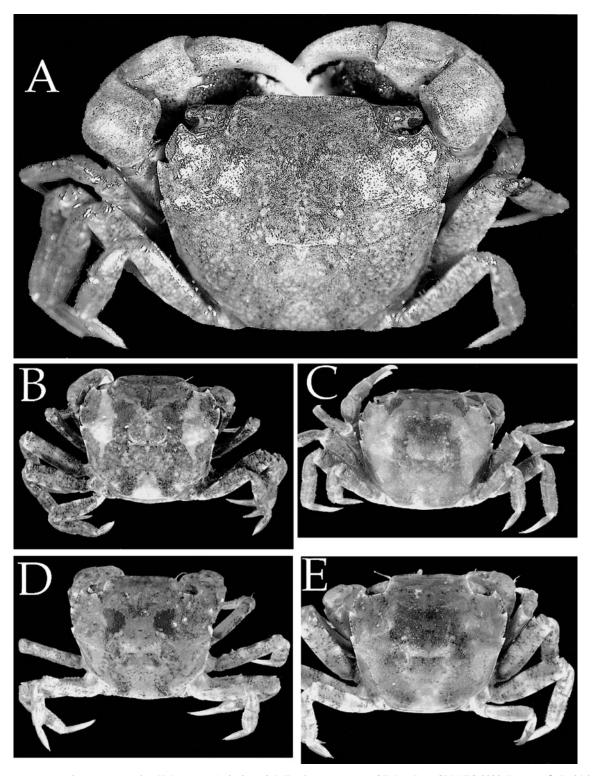


Fig. 1. Hemigrapsus takanoi, new species. Holotype  $\beta$ : A, 21.3  $\times$  18.4, Tomiura, east coast of Tokyo Bay, CBM-ZC 8039. Paratype  $\varphi$ : B, 24.2  $\times$  21.3; C, 21.2  $\times$  19.4; D, 22.4  $\times$  19.4; E, 19.0  $\times$  17.1; Kattoshi-misaki, Hokkaido, CBM-ZC 8044. All dorsal view.

of minute granules on lower half of outer surface continuing onto fixed finger. Large patch of dense soft setae present near bases of fixed finger and dactylus, extending distally 0.40–0.55 length of dactylus. Cutting edges of both fingers with several large teeth.

Female chelipeds (Fig. 7A) subequal, small and slender; chelae lacking patch of dense soft setae; otherwise similar to male.

Ambulatory legs (Figs. 4, 5) flattened, broad, third pair longest. Meri of first to third pairs each with dorsal margin

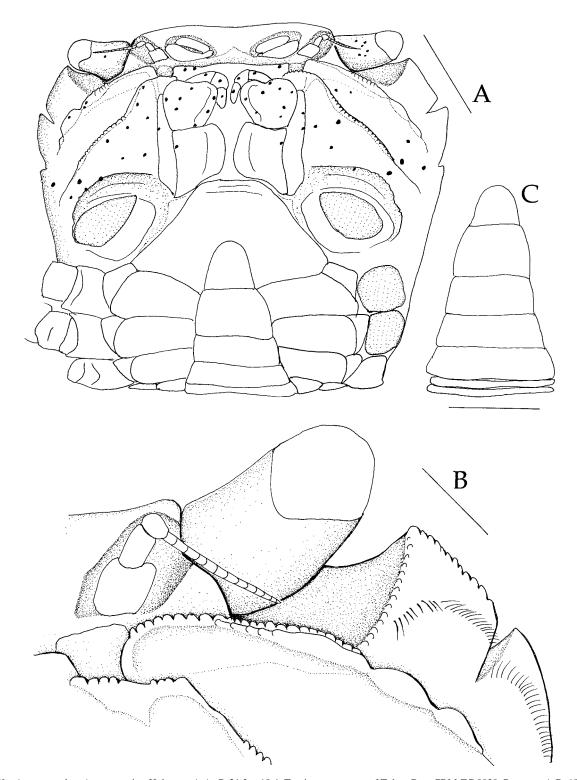


Fig. 2. Hemigrapsus takanoi, new species. Holotype 3: A, C,  $21.3 \times 18.4$ , Tomiura, east coast of Tokyo Bay, CBM-ZC 8039. Paratype 3: B,  $18.0 \times 16.2$ , Oui-futo, innermost of Tokyo Bay, CBM-ZC 8040. A, cephalothorax and abdomen, ventral; B, left anterior portion of cephalothorax, ventral; C, abdomen, ventral. Scales equal 4 mm for A and C and 1 mm for B.

bearing strong subdistal spine; meri of all legs with fine plumose setae on dorsal margins, denser proximally. Carpi unarmed; row of bristle-like setae present on distal margin of inner face, dorsal margin, near dorsal margin of outer face, and, in first pair, on distal half of median line of inner surface. Propodi each with 3 rows of bristle-like setae on dorsal surface and 2 rows of bristle-like setae on ventral surface sometimes accompanied by outer and inner rows of bristle-like setae in tufts; distal margin of dorsal face also fringed with bristle-like setae. Dactyli each with row of

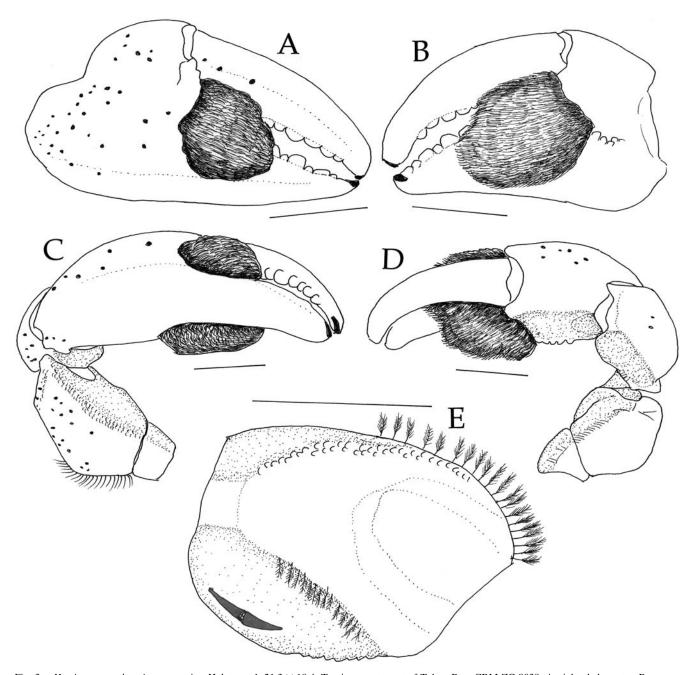


Fig. 3.  $Hemigrapsus\ takanoi$ , new species. Holotype  $3:21.3\times18.4$ , Tomiura, east coast of Tokyo Bay, CBM-ZC 8039. A, right chela, outer; B, same, inner; C, right cheliped, ventral; D, same, dorsal; E, merus of right cheliped, inner. Scales equal 4 mm.

bristle-like setae on ventral and dorsal margins; inner and outer surfaces also with dorsal and ventral rows of bristlelike setae; tips chitinous.

Male abdomen (Fig. 2C) narrowly triangular, 7-segmented; first and second segments very short; third through fifth segments trapezoidal, lateral margins straight; sixth segment longest, subtrapezoidal, lateral margins convex.

First pleopod of male (Fig. 6A, B) with distal, semicircular chitinous process, slightly curved dorsally outwards; setae on tip not curved.

Female abdomen (Fig. 7B) broad, rounded, 7-segmented; first and second segments very short; third through fifth

segments very broad, roundly subtrapezoidal, lateral margins convex; sixth segment longest, roundly subtrapezoidal, lateral margins convex.

Telson of male (Fig. 2C) subtriangular, margin convex, tip rounded; telson of female (Fig. 7B) very broadly subtriangular, margin convex.

Dorsal surfaces of carapace, chelipeds, and ambulatory legs dark grayish, greenish and/or brownish, but coloration of carapace occasionally varying (Fig. 1B–E); for example, large symmetrical white patches present, mostly in females or small individuals. Dark brown and/or purple spots present ventrally on cephalothorax, third maxillipeds, outer faces of

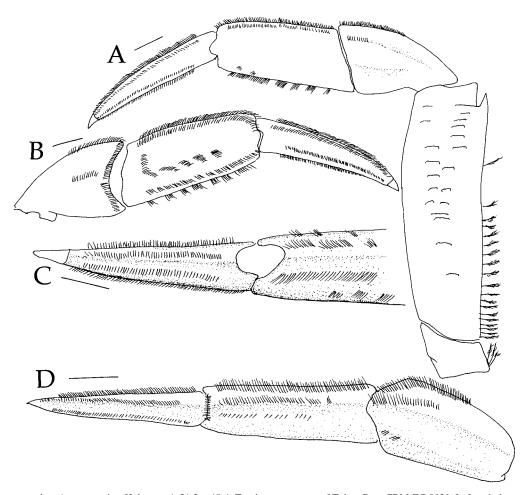


Fig. 4. *Hemigrapsus takanoi*, new species. Holotype 3: 21.3 × 18.4, Tomiura, east coast of Tokyo Bay, CBM-ZC 8039. Left ambulatory leg 1: A, whole, outer; B, dactylus, propodus and carpus, inner; C, dactylus and proximal portion of propodus, ventral; D, dactylus, propodus and carpus, dorsal. Scales equal 1 mm.

chelipeds, and sometimes ocular peduncles, but never on abdominal segments (Figs. 2A, 7B); spots comparatively smaller than those of *H. penicillatus*.

Affinities.—In addition to *H. takanoi* new species and *H. penicillatus*, three other species of *Hemigrapsus* have been recorded from Japan and adjacent waters: *H. sanguineus* (de Haan, 1835), *H. sinensis* Rathbun, 1929, and *H. longitarsus* (Miers, 1879).

Hemigrapsus sanguineus is separated from both *H. takanoi* and *H. penicillatus* by shape of the infraorbital ridge; the ridge of the former is finely striated, but that of the latter two species are more or less smooth and divided into three parts of unequal length. Additionally, male *H. sanguineus* is easily separated from both male *H. takanoi* and *H. penicillatus* in lacking setal patches on the chelae, but instead, it has a vesicle-like structure called pulvinus on each chela.

Hemigrapsus sinensis is separated from both H. takanoi and H. penicillatus in having the infraorbital ridge divided into a long inner ridge and a short, outer striated ridge. Further, both sexes of H. sinensis have setal patches on the chelae, but only males of H. takanoi and H. penicillatus have such setal patches.

In *H. longitarsus*, the carapace is pilose and as long as broad, its lateral borders are parallel, and the three anterolateral teeth are subequal in size, whereas in both *H. takanoi* and *H. penicillatus* the carapaces are almost naked, distinctly broader than long, their lateral boarders are arched, and the third anterolateral tooth is smaller than other two.

It is easy to separate *H. takanoi* and *H. penicillatus* if they are still alive or only recently fixed. Although an extensive color polymorphism is seen in the dorsal faces of the carapaces in both species, the color pattern on the ventral faces of the cephalothorax and abdomen in each species is constant and is apparently different between the two. In *H. penicillatus*, dark spots are present ventrally on the abdominal segments (Figs. 8, 10), but the dark spots do not occur on the abdominal segments of *H. takanoi* (Figs. 2A, 7). Moreover, the spots are larger in *H. penicillatus* (Figs. 8, 9A, E, 10A, E) than in *H. takanoi* (Figs. 2A, 3A, C, D, 7A, B).

As pointed out by Takano *et al.* (1997), the setal patches on the male chelipeds are much larger in *H. takanoi* (Fig. 3A–D) than in *H. penicillatus* (Fig. 9); the setal patch extends distally 0.40–0.55 the length of the dactylus in *H. takanoi*, but only 0.10–0.30 in *H. penicillatus* in the specimens examined in the present study (0.20–0.30 in the report by Takano *et al.* (1997). In particular, large

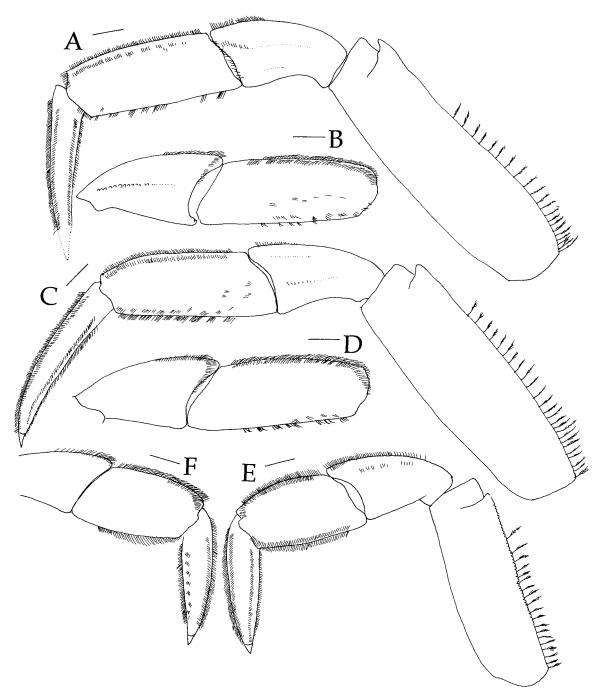


Fig. 5.  $Hemigrapsus\ takanoi$ , new species. Holotype  $\beta$ : 21.3  $\times$  18.4, Tomiura, east coast of Tokyo Bay, CBM-ZC 8039. Left ambulatory leg 2: A, dactylus through merus, outer; B, propodus and carpus, inner. Left ambulatory leg 3: C, dactylus through merus, outer; D, propodus and carpus, inner. Left ambulatory leg 4: E, dactylus through merus, outer; F, dactylus, propodus and distal portion of carpus, inner. Scales equal 1 mm.

individuals (CW > 20 mm) of H. penicillatus have very small setal patches.

The male first pleopod of *H. takanoi* (Fig. 6A, B) is comparatively stouter, and the chitinous process is less curved, than that of *H. penicillatus* (Fig. 6C, D); setae on the tip of the pleopod are nearly straight in *H. takanoi*, but they are recurved in *H. penicillatus*.

Females of both species are morphologically very similar and cannot be easily separated if the colour pattern has faded.

Etymology.—This species is named for Masatsugu Takano, who first recognized two distinct populations in *Hemigrapsus penicillatus*, *s. l.* 

Remarks.—The type series of Hemigrapsus penicillatus also includes specimens of H. takanoi. Examination of the black and white photographs of paralectotypes of Hemigrapsus penicillatus in Yamaguchi and Baba (1993) shows at least one male (fig. 178-B-e, p. 468, RMNH D 42130) has a large setal patch on each chela, and thus must belong to

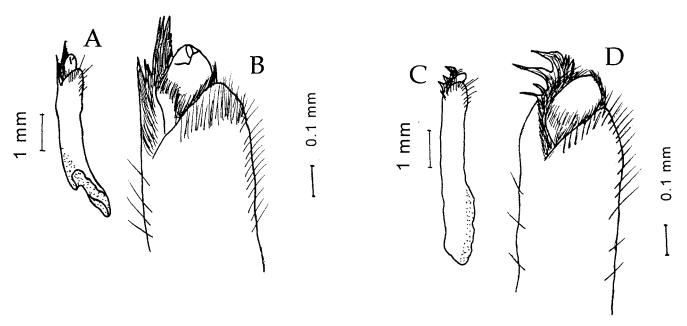


Fig. 6. A, B: Hemigrapsus takanoi, new species: paratype 3, 22.5 × 19.8, Kasai Rinkai Park, Tokyo Bay, CBM-ZC 8119. C, D: Hemigrapsus penicillatus (de Haan, 1835): 3, 19.9 × 18.7, Heguri River, Tateyama, Chiba, CBM-ZC 8120. Right first pleopod: A, C, whole; B, D, distal portion. Illustrations by Winda Mercedes Mingkid.

*H. takanoi*. Because all of this material has completely lost colour, we cannot determine the specific identity of the eight paralectotype females.

It is highly probable that material from Japan used by Miers (1886), Ortmann (1894), Stimpson (1907), Parisi (1918), Tesch (1918), Balss (1922), and Yokoya (1928) included both *H. takanoi* and *H. penicillatus*, because both species occur sympatrically.

Sakai's (1939, 1965, 1976) color illustration of "Hemigrapsus penicillatus" shows relatively large setal patches on the chelae, indicating that this specimen at least was *H. takanoi*. However, Sakai examined a considerable number of these very common crabs when he made his description (Muraoka, 1998), and it can be assumed he had a mixed collection of both *H. takanoi* and *H. penicillatus*. Sakai (1957), in his section of the "Color Encyclopedia of Invertebrates from Japan," also illustrated a "Hemigrapsus penicillatus" with larger setal patches, that is clearly *H. takanoi*.

Photographs of large males of "Hemigrapsus penicillatus" in Nishimura and Suzuki (1971, pl. 45-4), Miyake (1983), and Wada (1995), as well as Sakai's (1982) pen illustration of the same species, are all in dorsal view. As the size of the spotting and the setal patches on the chelae cannot be seen, species determination is impossible.

An unnumbered photograph of "Hemigrapsus penicillatus" in Takeda (1975), with comparatively large setal patches on the chelipeds, is clearly *H. takanoi*. Similarly, the large male crab depicted by Tsutsumi and Takemura (1980) as "Hemigrapsus penicillatus" has very small spots on the dorsal surface of the chelipeds, and large setal patches on the chelipeds, and should be referred *H. takanoi*.

Takeda's (1982) color illustration is only a slightly modified version of Sakai's (1976) illustration of "*H. penicillatus*" here re-identified as *H. takanoi*.

The black and white photographs of *H. penicillatus* in Aiyun and Siliang (1986, 1991) are very unclear, making species determination impossible. Similarly, the photograph of a male crab in Nishimura and Ito (1987) is too small to allow identification. The large male crab in the photograph of Takeda and Kawashima (1997) shows very small spots on the ventral surface of the carapace and third maxillipeds, indicative of *H. takanoi*. The frontal view photograph of a female "*Hemigrapsus sanguineus*" in Nishimura and Suzuki (1971: pl. 45-3), showing small spots on the chelipeds, on the ventral surface of the carapace, and on the third maxillipeds, is also of *H. takanoi*.

The record of *H. penicillatus* from Hawaii by Edmondson (1959) cannot be confirmed. His crustacean material was originally lodged in the Bernice P. Bishop Museum; however, his "*H. penicillatus*" material is apparently lost (see Marine Invertebrate Databases: http://www.bishopmuseum.org/research/natsci/invert/invertdata.html).

*Habitat.*—Found under boulders and other hard structures in intertidal areas of mud flats, estuaries, lagoons, and sheltered beaches. Generally found in more wave-sheltered areas than *H. penicillatus*, although the two species often occur sympatrically.

Distribution.—Takano et al. (1999) confirmed the distribution of this species in Honshu, Shikoku, and Kyushu. According to an independent web-site (Sapporo Crab Info: http://www.zspc.com/crab/kefusa/index.html), this species has also been found in Ishikari Bay, Hokkaido. Hemigrapsus penicillatus, s. l., has been previously recorded from Sakhalin Island (Russia), Okinawa, Taiwan, Korea, northern China and Hawaii (unconfirmed), but the distribution of H. takanoi in those waters remains unconfirmed.



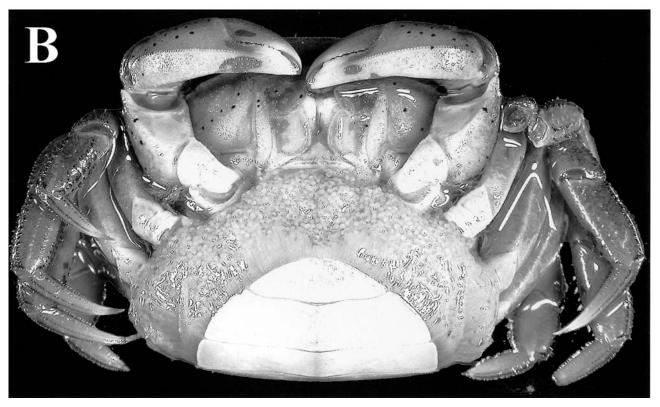


Fig. 7. Hemigrapsus takanoi, new species. Paratype  $\cite{poisson}$ : 19.0  $\times$  16.5 mm, Oui-futo, innermost of Tokyo Bay, CBM-ZC 8040. A, chelipeds, outer; B, whole, ventral.

The recent accidental introduction of "Hemigrapsus penicillatus" into European waters was first reported by Noël et al (1997). Since 1993, the species has been found at Bremer, Germany, and the Netherlands, as well as various localities along the coasts of Belgium, France, and Spain (Bay of Biscay)(d'Udekem, 1998, 1999; Gollasch, 1999; Vincent and Breton, 1999; Nijland and Beekman, 2000; Vincent and Noël, 2002; Breton et al., 2002; Nijland, 2003; Dumoulin, 2004; Campbell and Nijland, 2004). D'Udekem and Faasse (2002) and Dumoulin (2004) have provided a detailed history of the invasion of this species in Europe.

According to d'Udekem and Faasse (2002), specimens from the Bay of Biscay were identified by M. Takano as belonging to form II of Takano *et al.* (1997) (= *H. takanoi*). Furthermore, examination by d'Udekem (personal communication in 2004) on the abundant material from France and

the Netherlands collected by him and his colleagues has shown that all of them are definitely *H. takanoi* only, because the specimens have small dots on the ventral side, and the dots are never seen on the abdominal segments. The first author (AA) also examined and identified a male and a female *H. takanoi* in the Natural History Museum, London, that had been collected by P. Noël from the French coast. There are also several color photographs of "Hemigrapsus penicillatus" on a web site detailing its recent invasion of the Netherlands (De Penseelkrab: http://www.krabben.net/ reindert/old/penseelkrab/hemigrapsus.htm), but judging from the size of the setal patches on the chelae, the crabs figured include at least one male H. takanoi. Therefore, it appears that it is H. takanoi rather than H. penicillatus that has invaded the coasts of France, Spain, Belgium and the Netherlands.

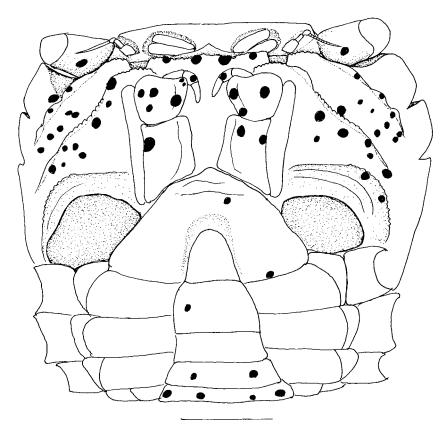


Fig. 8. Hemigrapsus penicillatus (de Haan, 1835). 3: 17.1 × 15.0, Tomiura, east coast of Tokyo Bay, CBM-ZC 8047. Ventral face of cephalothorax and abdomen. Scale equals 4 mm.

## Hemigrapsus penicillatus (de Haan, 1835) Figs. 6D, 8–10

Grapsus (Eriocheir) penicillatus de Haan, 1835: 60, pl. 11, fig. 5 (in part). Brachynotus penicillatus.—Miers, 1886: 264 (in part?).—Tesch, 1918: 104 (in part?).—Balss, 1922: 150 (in part?).

Heterograpsus penicillatus.—Ortmann, 1894: 714 (in part?).—Parisi, 1918: 101 (in part?).

Hemigrapsus penicillatus.—Stimpson, 1907: 126 (on foot-note) (in part?).—Shen, 1932: 163, text-figs. 104, 105, pl. 7, fig. 2 (in part?).—Sakai, 1939: 673 (in part?).—Kamita, 1941: 204, text-figs. 113a, b (in part?).—Miyake, 1961: 176 (list).—Miyake et al., 1962: 130 (in part?).—Sakai, 1965: 198. (in part?).—?Nishimura and Suzuki, 1971: pl. 45-4, 124.—Sakai, 1976: 650 (English Part) (in part?), 403 (Japanese Part) (in part?).—Kikuchi and Miyake, 1978: 44 (list) (in part?).—Sakai, 1982: 717 (?).—Takeda, 1982, 218, fig. 647.—Miyake, 1983: 175, pl. 59-4 (?).—Sakai and Nakano, 1983: 88 (in part?).—Aiyun and Siliang, 1986: 478 (key), 478, figs. 269-2, 269-3, pl. 67-5 (?)—Nishimura and Ito, 1987: 123 (unnumbered photo), 124 (?).—Yamaguchi et al., 1987: 31 (in part?), pl. 15, fig. 2a, 2b (in part?), 2c, 2d.—Inaba, 1988: 107 (in part?).—Fukui *et al.*, 1989: 229, 236 (list) (?).—Takeda and Hayashi, 1990: 56 (?).— Aiyun and Siliang, 1991: 524 (key), 525, figs. 269-2, 269-3, pl. 67-5 (?).—Yamaguchi and Baba, 1993: 178, figs. 178A, 178-B, 178-C (in part).—Wada, 1995: pl. 114, fig. 7, 408 (in part?).—Muraoka, 1998: 53 (in part?).—Kobayashi, 2000: 216.—Yamaguchi and Baba, 2003: 58.

Brachynotus brevidigitalis.—Yokoya, 1928: 780, text-fig 8 (in part?).

Not Hemigrapsus penicillatus.—Sakai, 1939: pl. 75, fig. 1.—Sakai, 1957: 82, pl. 41.—Sakai, 1965: pl. 94, fig. 3.—Takeda, 1975: 146 (unnumbered photo).—Sakai, 1976: pl. 222, fig. 2.—Tsutsumi and Takemura, 1980: 137.—Takeda, 1982: 218, fig. 647.—Yamaguchi and Baba, 1993: fig. 178-B (upper left male).—Takeda and Kawashima, 1997: 216.—Noël et al., 1997: 741.—Breton et al., 2002: 187, fig. 2B.—d'Udekem d'Acoz and Faasse, 2002: 107, figs. 2B, 3B, 4. [= Hemigrapsus takanoi, new species.]

?Hemigrapsus penicillatus.—Edmondson, 1959: 180, fig. 14.
 Hemigrapsus sanguineus.—Nishimura and Suzuki, 1971: pl. 45-3. [not Hemigrapsus sanguineus (de Haan).]

Material Examined.—23, 28.7 × 14.2–38.7 × 26.2, Orikasa-gawa River, Yamada-machi, Shimohei-gun, Iwate Pref., HON, PACIFIC, 1 Aug. 1993, coll. N. Nunomura, TOYA Cr 13052-13053 (Z93-25); 33, 17.9 × 15.6- $24.9 \times 21.2$ ,  $6^{\circ}_{+}$ ,  $18.6 \times 15.8$ – $22.8 \times 20.7$ , river mouth, Oritate-gawa River, under boulders, Shizugawa-cho, Motoyoshi-gun, Miyagi Pref., HON, PACIFIC, 20 July 2004, coll. K. Tanaka, CBM ZC-8046; 13, 17.1 × 15.0, intertidal, estuary of Okamoto-gawa, Tomiura, Chiba Pref., Boso Peninsula, east coast of Tokyo Bay, HON, PACIFIC, 9 Aug. 2002, coll. Satoshi Akiwa, CBM-ZC 8047; 10♂, 13.4 × 11.8–22.4 × 19.1, 9♀, 10.4 × 9.2-18.8 × 15.8, intertidal, estuary, Heguri-gawa, Tateyama-shi, Chiba Pref., Boso Peninsula, HON, PACIFIC, 12 June 2002, coll. Satoshi Akiwa, CBM-ZC 8048; 13, 19.9 × 18.7, intertidal, estuary, Heguri-gawa, Tateyama-shi, Chiba Pref., Boso Peninsula, HON, PACIFIC, 22 Apr. 2004, coll. Winda Mercedes Mingkid, CBM-ZC 8120; 153, 13.2 × 11.8- $21.5 \times 18.6, 14^{\circ}, 14.5 \times 13.9 - 20.3 \times 17.5$ , intertidal, mouth of Kanaya River, Hamakanaya, Chiba Pref., Boso Peninsula, east coast of Tokyo Bay, HON, PACIFIC, 21 Aug. 2002, coll. Satoshi Akiwa, CBM-ZC 8049; 95,  $9.9 \times 8.9 - 16.6 \times 14.1$ ,  $7^{\circ}$ ,  $10.1 \times 9.0 - 13.6 \times 11.7$ , intertidal, mouth of Tsurumi river, under Tsurumi Ohashi Bridge, Yokohama-shi, Kanagawa Pref., innermost of Tokyo Bay, HON, PACIFIC, 26 Aug. 2002, coll. Satoshi Akiwa, CBM-ZC 8050; 7♂, 15.9 × 9.3–23.5 × 19.4, 10♀, 10.2 × 9.0–16.1 × 14.4, intertidal, Kannon-zaki, Miura Peninsula, Kanagawa Pref., west coast of Tokyo Bay, HON, PACIFIC, 12 June 2002, coll. Satoshi Akiwa, CBM-ZC 8051; 43,  $9.1 \times 7.7 - 28.7 \times 25.5$ , 22,  $14.5 \times 13.2 - 16.7 \times 13.2 \times 13.2$ 14.7, intertidal, Ena Bay, Miura Peninsula, Kanagawa Pref., west coast of Tokyo Bay, HON, PACIFIC, 25 July 2002, coll. Satoshi Akiwa, CBM-ZC 8052; 43,  $13.7 \times 12.3 - 19.1 \times 17.1$ , 29,  $14.8 \times 13.2 - 16.6 \times 14.6$ , intertidal, Tenjin-jima, Yokosuka-shi, Miura Peninsula, Kanagawa Pref., HON, PACIFIC, 20 July 2004, coll. T. Kuramochi, HSM-crb-600; 19, 14.1 × 12.4, intertidal, Ena Bay, Miura-shi, Miura Peninsula, Kanagawa Pref., HON, PACIFIC, June 2001, coll., H. Ikeda, HSM-crb-599; 13, 12.2 × 10.9, Iwasehama, Toyama-shi, Toyama Pref., HON, SEA-JAPAN, 2 July

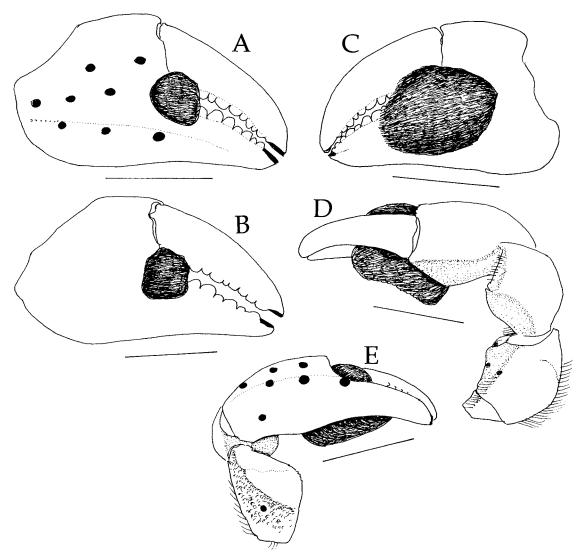


Fig. 9. Hemigrapsus penicillatus (de Haan, 1835). A, C–E: 3, 17.1 × 15.0, Tomiura, east coast of Tokyo Bay, CBM-ZC 8047; B: lectotype 3, Japan, RMNH D 200 (by C. H. J. M. Fransen). A, B, right chela, outer; C, same, inner; D, right cheliped, dorsal; E, same, ventral. Scales equal 4 mm.

1990, coll. N. Nunomura, TOYA Cr 13054 (Z90-32); 1♀, 18.8 × 17.0, Iwasehama, Toyama-shi, Toyama Pref., HON, SEA-JAPAN, 21 Oct. 1990, coll. N. Nunomura, TOYA Cr 10180 (Z90-58); 23, 19.5  $\times$  17.3–26.0  $\times$ 22.9, 12, 21.4 × 18.5, Kurosaki, Nanao-shi, Ishikawa Pref., HON, SEA-JAPAN, 2 Sept., 1980, coll. H. Nanbu, TOYA Cr 3128-3130 (Z80-114); 13, 21.9 × 18.9, Tassha, Aikawa-machi, Sado-gun, Niigata Pref., HON, SEA-JAPAN, 19 Apr. 1989, coll. H. Nanbu, TOYA Cr 8766 (Z89-8); 13, 19.2 × 16.2, Higashihanzu, Hanzu-cho, Hanzu-gun, Aichi Pref., HON, PACIFIC, 15 Dec. 1989, coll. H. Nanbu, TOYA Cr 8934–8937; 23, 8.5 × 7.6–12.5 × 9.7, river mouth, Kashi River, Sennan-shi, Osaka-fu, HON, SETO, coll. R. Yamanishi, OMNH Ar 2947 (Z85-10); 23, 21.1 × 19.8-27.9  $\times$  24.0, 3 $^{\circ}$ , 18.5  $\times$  16.2–28.4  $\times$  24.0, under boulders, under Yodogawa-ohashi Bridge, Ebie, Fukushima-ku, Osaka-shi, Osaka-fu, HON, SETO, 15 Apr. 1987, coll. R. Yamanishi, OMNH Ar 3125 (Z87-16); 2♂, 20.5 × 18.4–21.1 × 18.9, 1 $\stackrel{\bigcirc}{}$ , 19.1 × 17.0, Nishihiro-kaigan, Aritagun, Wakayama Pref., Kii Peninsula, HON, PACIFIC, 2 May 1996, coll. R. Yamanishi, OMNH Ar 3888 (Z96-29); 2♂, 9.6 × 8.1–19.9 × 17.2, 2♀, 18.8 × 16.6-19.7 × 17.4, river mouth, Yoshi-kawa River, Taiji-cho, Higashimuro-gun, HON, Wakayama Pref., PACIFIC, 7 Aug. 1995, coll. H. Hato'oka, OMNH Ar 3871; 5\$\operats\$, 14.5  $\times$  8.1–21.1  $\times$  22.5, 4\$\operats\$, 11.6  $\times$  10.4– 24.7 × 22.5, river mouth, Koya-gawa River, Koyagawa, Shimonoseki-shi, Yamaguchi Pref., HON, SETO, 23 May 1994, coll. R. Yamanishi, OMNH Ar 4513 (Z00-33); 1♂, 23.7 × 20.6, Otonashi, Uranouchi, Susaki-shi, Kochi Pref., SHI, PACIFIC, 30 May 1980, coll. R. Yamanishi, OMNH Ar 2497

(Z80-38); 23,  $16.5 \times 9.2$ – $27.4 \times 23.1$ , river mouth, Midori River, Sumiyoshi, Kumamoto Pref., KYU, SEA-JAPAN, coll. Osaka-wan Kaiganseibutsu Kenkyukai (= Research Club of Marine Organisms in Osaka Bay), SEA-JAPAN, 17 May 1999, OMNH Ar 4342 (Z99-42).

Description.—Male chelipeds each with patch of dense soft setae present near bases of fixed finger and dactylus, extending distally 0.10–0.30 length of dactylus. Male first pleopod less stout and tip of chitinous process more curved than that of *H. takanoi*; setae on tip recurved. Dark brown and/or purple spots present ventrally on cephalothorax, third maxillipeds, abdominal segments, outer faces of chelipeds, and sometimes ocular peduncles; spots comparatively larger than those of *H. takanoi*. Other morphological features and coloration similar to those of *H. takanoi*.

Remarks.—The crabs depicted by Yamaguchi et al. (1987: figs. 2c, 2d) and Kobayashi (2000: 216) have the larger spots on the ventral surface of the carapace and chelipeds, and the smaller setal patches on the chelipeds, that are



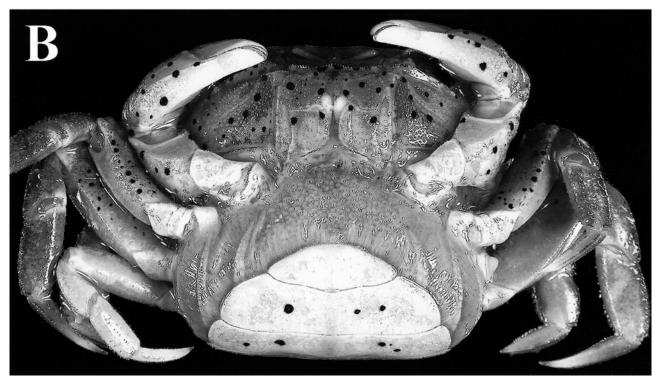


Fig. 10. Hemigrapsus penicillatus (de Haan, 1835). ♀, 16.8 × 14.2 mm, Tateyama-shi, east coast of Tokyo Bay, CBM-ZC 8048. A, chelipeds, outer; B, whole, ventral.

typical of *Hemigrapsus penicillatus* (see "Remarks" under *H. takanoi*).

*Habitat.*—Found under boulders and other hard structures in intertidal areas of mud flats, estuaries, lagoons, and sheltered beaches.

Distribution.—Takano et al. (1999) confirmed the distribution of this species around Honshu, Shikoku and Kyushu. Hemigrapsus penicillatus, s. l., has been previously recorded from Sakhalin Island (Russia), Okinawa, Taiwan, Korea, northern China, and Hawaii (unconfirmed) (see discussion of distribution under H. takanoi).

### ACKNOWLEDGEMENTS

We are especially grateful to Satoshi Akiwa (Tokyo University of Marine Science and Technology) for making material available for study and providing information on the geographical distribution of the two species in Tokyo Bay, and to Winda Mercedes Mingkid (TUMST) for information and illustrations of the male first pleopods of the two species. We also

express our sincere appreciation to Masatsugu Takano (Tamano Station, National Center for Stock Enhancement) and Minoru Ikeda (Laboratory of Applied Population Genetics, Tohoku University), who first recognized two distinct populations in Hemigrapsus penicillatus, s. l., provided us with the opportunity to describe them, and made very useful comments on an earlier draft of the manuscript. We are also grateful to the following persons for the loan of, or collecting, material; Ryohei Yamanishi (OMNH), Noboru Nunomura (TOYA), Takashi Oba (Hokkaido University), Jun Ohtomi (Kagoshima University), and Katsuhiko Tanaka (Shizugawa Nature Center, Miyagi). Reindert Nijland (Rijksuniversiteit Groningen), Emmanuel Dumoulin (Belgium), and Cédric d'Udekem d'Acoz (Tromsø Museum, University of Tromsø) kindly provided us with necessary literature. Careful reviews by Peter J. F. Davie (Queensland Centre for Biodiversity, Queensland Museum), C. d'Udekem d'Acoz, and Paul Clark (NHM) greatly improved the earlier draft of the manuscript. Special thanks are due to Charles H. J. M. Fransen (RMNH) for information on type material and for sketching the lectotype of H. penicillatus. Cédric d'Udekem d'Acoz graciously provided information on the recent invasion of H. penicillatus into European waters and helped the first author (AA) to translate Dutch into English. Paul Clark generously facilitated examination of invasive H. penicillatus during the first author's stay in NHM. Furthermore, we are also indebted to Keiji Wada (Nara Women's University) and other reviewers for their critically useful comments on the final draft.

### LITERATURE CITED

- Aiyun, D., and Y. Siliang. 1986. Crabs of the China Seas. China Ocean Press, Beijing. 642 pp. [In Chinese.]
- ——, and ——. 1991. Crabs of the China Seas. China Ocean Press, Beijing, and Springer–Verlag, Berlin. 682 pp. [English translation version.]
- Balss, H. 1922. Ostasiatische Decapoden. IV. Brachyrhynchen (Cancridae).—Archiv für Naturgeschichte 88: 94–166, pls. 1–2.
- Breton, G., M. A. Faasse, P. Y. Noël, and Th. Vincent. 2002. A new alien crab in Europe: *Hemigrapsus sanguineus* (Decapoda: Brachyura: Grapsidae).—Journal of Crustacean Biology 22: 184–189.
- Campbell, S., and R. Nijland. 2004. De Blaasjeskrab, *Hemigrapsus sanguineus* (De Haan, 1835), voor het eerst op het Nederlandse strand.—Het Zeepaard 64: 40–44.
- Dumoulin, E. 2004. Snelle areaaluitbreiding van het penseelkrabbetje Hemigrapsus penicillatus (de Haan, 1835) langs de kusten van de Zuidelijke Bocht van de Noordzee, status van haar opmars in de Westerschelde en beschouwingen over de ecologie en het gedrag van de soort.—De Strandvlo 24: 5–35.
- Edmondson, C. H. 1959. Hawaiian Grapsidae.—Occasional Papers of the Bernice P. Bishop Museum 22: 153–202.
- Fukui, Y., K. Wada, and C.-H. Wang. 1989. Ocypodidae, Mictyridae and Grapsidae (Crustacea: Brachyura) from coasts of Taiwan.—Journal of Taiwan Museum 42: 225–238.
- Gollasch, S. 1999. The Asian decapod *Hemigrapsus penicillatus* (de Haan, 1835) (Grapsidae, Decapoda) introduced in European waters: status quo and future perspective.—Helgolander Meersuntersuhungen 52: 359–366.
- de Haan, W. 1833–1850. Crustacea. Pp. i–xxxi, ix–xvi, 1–243, pls. A–J, L–Q, 1–55, tables 1–2 in I. P. F. von Siebold. Fauna Japonica sive Descriptio Animalium, quae in itinere per Japoniam, jussu et auspiciis superiorum, qui summum in India Batavia imperium tenent, suscepto, annis 1823–1830 collegit, notis, observationibus et adumbrationibus illustravit P. F. de Siebold. Conjunctis studiis C. J. Temminck et H. Schlegel pro Vertebratis atque W. de Haan pro Invertebratis elaborata Regis aupicus edita. Lugduni-Batavorum, Leiden.
- Inaba, A. 1988. Fauna and Flora of the Seto Inland Sea II (second edition). Mukaishima Marine Biological Station, Faculty of Science, Hiroshima University, Mukaishima. 475 pp. [In Japanese.]
- Kamita, T. 1941. Studies of the Decapod Crustaceans of Chosen. Part I. Crabs. The Fisheries Society of Chosen, Keijo. 289 pp., 1 map.
- Kikuchi, T., and S. Miyake (eds.). 1978. Fauna and Flora of the Sea around the Amakusa Marine Biological Laboratory: Decapod Crustacea (revised edition). The Amakusa Marine Biological Laboratory, Kyushu University, Amakusa. 52 pp. [In Japanese.]
- Knowlton, N. 1986. Cryptic and sibling species among the decaped Crustacea.—Journal of Crustacean Biology 6: 356–363.
- ——. 1993. Sibling species in the sea.—Annual Review of Ecology and Systematics 24: 189–216.
- Kobayashi, Y. 2000. Life in the Seashore (Umibe no Ikimono). Yama-kei, Pocket Guide, Yama to Keikoku sha, Tokyo. 282 pp. [In Japanese.]
- Mayr, E. 1963. Animal Species and Evolution. Harvard University Press, Cambridge. 797 pp.
- Miers, J. E. 1879. On a collection of Crustacea made by Capt. H. C. St. John. R. N. Corean and Japanica Seas.—Proceedings of the Zoological Society of London 1879: 18–61, pls. 1–3.
- ———. 1886. Report on the Brachyura collected by H. M. S. *Challenger* during the years 1873–76. Report on the scientific results of the voyage of H. M. S. *Challenger* during the years 1873–76, Zoology 17: i–l + 1–362 pp.
- Miyake, S. 1961. A list of the decapod Crustacea of the Sea of Ariaké, Kyushu.—Records of Oceanographic Works in Japan, Special Number 5: 165–178
- ——. 1983. Japanese Crustacean Decapods and Stomatopods in Color. II Brachyura (Crabs). Hoikusha, Osaka. 261 pp. [In Japanese.]
- K. Sakai, and S. Nishikawa. 1962. A fauna-list of the decapod Crustacea from the coasts washed by the Tsushima Warm Current.— Records of Oceanographic Works in Japan, Special Number 6: 121–131.
- Muraoka, K. 1998. Catalogue of the brachyuran and anomuran crabs donated by Prof. Dr. Tune Sakai to the Kanagawa Prefectural Museum.—Catalogue of the Collection in the Kanagawa Prefectural Museum of Natural History 11: 13–67 [In Japanese.]
- Nijland, R. 2003. Hemigrapsus penicillatus: Een nieuwe krab in Nederland.—Natura 100: 72–74.

- ——, and J. Beekman. 2000. *Hemigrapsus penicillatus* De Haan 1835 waargenomen in Nederland.—Het Zeepaard 60: 169–171.
- Nishimura, S., and K. Ito. 1987. Seashore Animals (Kaigan Doubutsu). Hoikusha, Osaka. 207 pp. [In Japanese.]
- ——, and K. Suzuki. 1971. Common Seashore Animals of Japan in Color (Kaigan Dobutsu). Hoikusha, Osaka. 196 pp. [In Japanese.]
- Noël, P. Y., E. Tardy and C. d'Udekem d'Acoz. 1997. Will the crab Hemigrapsus penicillatus invade the coasts of Europe?—Comptes Rendus de l'Académie des Sciences Paris, Sciences de la Vie / Life Sciences 320: 741–745.
- Ortmann, A. 1894. Crustaceen. Semon Zoologische Forschungsreisen in Australien und dem Malayischen Archipel, V.—Denkschriften der Medizinischen naturwissensch Gesellschaft 8: 1–80.
- Parisi, B. 1918. I Decapodi giapponesi del Museo di Milano. VI. Catometopa e Paguridea.—Atti della Societa Italiana de Scienze Naturali 57: 5–42 pls. 7–11.
- Rathbun. 1929. New and rare Chinese crabs.—Lingnan Science Journal, Lingnan University 8: 75–104 pls. 5–15.
- Sakai, K., and T. Nakano. 1983. List of decapod Crustacea in Laboratory of Crustacea, Shikoku Women's University, Tokushima. I.—Bulletin of Shikoku Women's University 33: 73–94 [In Japanese.]
- Sakai, T. 1939. Studies on the Crabs of Japan. IV. Brachygnatha, Brachyrhyncha. Yokendo, Tokyo. 377 pp. (pagination number 365–741), 70 pls. (plate number 42–111).
- 1957. Brachyura. Pp. 29–86, plates 14–43 in Y. Okada, ed. Encyclopedia Zoologica. Nakayama-shoten, Tokyo.
- ——. 1965. The Crabs of Sagami Bay Collected by His Majesty the Emperor of Japan. The Imperial Household, Tokyo. 206 pp. (English part) + pls. 100 + 92 pp. (Japanese part) + 11 pp. (Bibliography) + 32 pp. (Index) + 1 map.
- ———. 1976. Crabs of Japan and the Adjacent Seas. Kodansha, Tokyo. 649 pp. (English part) + 461 pp. (Japanese part) + 251 plates.
- ——. 1982. Brachyura. Pp. 653–721 *in* T. Uchida, ed. New Illustrated Encyclopedia of the Fauna of Japan (Shin Nihon Doubutsu Zukan). Hokuryukan, Tokyo. [In Japanese.]
- Shen, C. J. 1932. The brachyuran Crustacea of north China.—Zoologica Sinica, series A, Invertebrates of China 9: 1–320 pls. 1–10.
- Stimpson, W. 1907. Report on the Crustacea (Brachyura and Anomura) collected by the North Pacific Exploring Expedition, 1853–1856.— Smithsonian Miscellaneous Collections 49: 1–240, 1–26 pls.
- Takano, M., M. Ikeda, and Y. Fujio. 1999. Geographical distribution patterns of two forms of *Hemigrapsus penicillatus* (De Haan).—Abstract for the Meeting of the Japanese Society of Fisheries Science, April 1–5, 1999: 119. [Abstract.]
- —, and A. Kijima. 1997. Biochemical and morphological evidence of two sympatric forms, interpreted as sibling species, in the estuarine grapsid crab *Hemigrapsus penicillatus* (De Haan).—Benthos Research 52: 111–117.
- Takeda, M. 1975. Suborder Brachyura. Pp. 120–149 in F. Utinomi ed. Aquatic Animals in Color (Suisei Doubutsu). Gakken, Tokyo. [In Japanese.]
- ——. 1982. Keys to the Japanese and Foreign Crustaceans Fully Illustrated in Color. Hokuryukan, Tokyo. 284 pp. [In Japanese.]
- ———, and H. Hayashi. 1990. Biogeographical notes on the anomuran and brachyuran crustaceans from the Pacific coasts of eastern Hokkaido, northern Japan.—Bulletin of Biogeographical Society of Japan 45: 45–59 [In Japanese.]
- ——, and K. Kawashima. 1997. Seashore Life (Umibe no Ikimono). Seibido Handy Library, Seibido, Tokyo. 448 pp. [In Japanese.]
- Tesch, J. J. 1918. The Decapoda Brachyura of the Siboga-Expedition. I. Hymenosomidae, Retroplumidae, Ocypodidae, Grapsidae, and Gecarcinidae.—Siboga-Expeditie Monographie 39c: 1–148 pls. 1–6.
- Tsutsumi, T., and Y. Takemura. 1980. Seashore Animals in Color (Genshoku Umibe no Doubustu). Ienohikari Kyokai. 230 pp. [In Japanese.]
- Udekem d'Acoz, C. d'. 1998. Kolonisatie van de Europees-Atlantische kusten door de borstelkrab *Hemigrapsus penicillatus* (de Haan, 1835).— De Strandvlo 18: 45–48.
- . 1999. Inventaire et distribution des crustacés décapodes de l'Atlantique nord-oriental, de la Méditerranée et des eaux continentales adjacentes au nord de 25°N.—Patrimoines Naturels (Muséum National d'Histoire Naturelle, Service du Patrimoine Naturel, Paris) 40: i–x + 1–383.

- ——, and M. Faasse. 2002. De huidige status van *Hemigrapsus sanguineus* (de Haan, 1835) en *H. penicillatus* (de Haan, 1835) in de noordelijke Atlantische Oceaan, in het bijzonder in Nederland, met opmerkingen over hun biologie (Crustacea, Decapoda, Brachyura).—Het Zeepaard 62: 101–115.
- Vincent, Th., and G. Breton. 1999. Présence du crabe *Hemigrapsus penicillatus* (de Haan, 1835) dans les bassins du port du Havre (Normandie, France).—Bulletin Trimestriel de la Société Géologique de Normandie et des Amis du Muséum du Havre 86: 19–23.
- —, and P. Y. Noël. 2002. Les mysidacés et décapodes capturés, collectés et observés entre 1978 et 2000 dans le port du Havre (Seine-Maritime, France).—Bulletin Trimestriel de la Société Géologique de Normandie et des Amis du Muséum du Havre 87: 71–91.
- Wada, K. 1995. Infraorder Brachyura. Pp. 379–418, pls 101–118 in S. Nishimura, ed. Guide to the Seashore Animals of Japan with Color Pictures and Keys. Volume 2. Hoikusha, Osaka. [In Japanese.]
- Watanabe, S. 2003. Structure and distribution of crustacean resources. Pp. 94–108 *in* J. Otomi and S. Watanabe, eds. Crustacean Resources and their Diversity. Kouseisha Kouseikaku, Tokyo. [In Japanese.]
- Yamaguchi, T. 1993. The contributions of von Siebold and H. Bürger to the natural history of Japanese Crustacea. Pp. 15–144 in T. Yamaguchi, ed.

- Ph. F. von Siebold and Natural History of Japan: Crustacea. The Carcinological Society of Japan, Tokyo.
- ——, and K. Baba. 1993. Crustacean specimens collected in Japan by Ph. F. von Siebold and H. Bürger and held by the Nationaal Natuurhistorisch Museum in Leiden and other museums. Pp. 145–570 in T. Yamaguchi, ed. Ph. F. von Siebold and Natural History of Japan: Crustacea. The Carcinological Society of Japan, Tokyo.
- —, and —. 2003. Crustacean specimens collected in Japan by Ph. F. von Siebold and H. Bürger and held by the Nationaal Natuurhistorisch Museum in Leiden and other museums (revised edition).—Calanus, Bulletin of the Aitsu Marine Station, Kumamoto University, Special Number 4: 3–86
- , K. Harada, M. Takeda and T. Kikuchi. 1987. Crab fauna of the Amakusa Islands.—Calanus, Bulletin of the Aitsu Marine Station, Kumamoto University 10: 1–71.
- Yokoya, Y. 1928. Report of the biological survey of Mutsu bay. 10. Brachyura and crab-shaped Anomura.—Science Report from the Tohoku Imperial University, series 4, 3: 757–784, text figs 1–8.

RECEIVED: 7 May 2004. ACCEPTED: 7 December 2004.