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Systematic Notes on the Pinnotherid Crabs of the Genus *Pinnaxodes* (Crustacea: Decapoda: Brachyura)

Masatsune Takeda[1] and Prince Masahito[2]

[1] Department of Zoology, National Science Museum, 3–23–1 Hyakunin-cho, Shinjuku-ku, Tokyo, 169–0073 Japan E-mail: takeda@kahaku.go.jp
[2] Higashi, Shibuya-ku, Tokyo, 150–0011 Japan

Abstract *Pinnaxodes major* Ortmann, 1894 and *P. mutuensis* Sakai, 1939, the West Pacific representatives of the genus *Pinnaxodes* Heller, 1865 (Crustacea, Decapoda, Pinnotheridae), are compared with the type species, *P. chilensis* (H. Milne Edwards, 1837) from Chile. The former is congeneric with the type species, but the latter is transferred to the genus *Holothuriophilus* Nauck, 1880. Otherwise, the systematic status of the other *Pinnaxodes* species is discussed.

Key words: Pinnotherid crabs, *Pinnaxodes*, *Holothuriophilus*, West Pacific, Chile.

Introduction

Pinnaxodes chilensis (H. Milne Edwards, 1837) of the Family Pinnotheridae, a peculiar pea crab inhabiting the recta of sea urchins from the west coast of South America, is well known to Chileans as a delicacy, and marine biologists are also interested in its peculiar mode of life and high percentage of parasitism. Up to date, in addition to the type species, *P. chilensis*, the genus *Pinnaxodes* established by Heller (1865) is represented by *P. floridensis* Wells et Wells, 1961 from Florida in the central West Atlantic, *P. gigas* Green, 1992 from the coast of Mexico in the central East Pacific, and *P. major* Ortmann, 1894 and *P. mutuensis* Sakai, 1939 from Japan, Korea and the Russian Far East in the northern West Pacific. The genus *Pinnaxodes* has been thus considered to be valid, but not always clearly distinguished from the genus *Pinnotheres* Bosc, 1802 and some related genera.

When one of the authors, Prince Masahito, visited the Chinquihue Foundation, Puerto Montto, Chile, on 26 September 1997, after participating in a ceremony and events celebrating the centennial friendship between Chile and Japan in Santiago, 13 specimens of pinnotherid crab, *Pinnaxodes chilensis* (H. Milne Edwards), which were collected from the recta of sea urchins, were donated to him by Mr. Rafael Herrea Zuniger, General Manager of the Foundation, for detailed taxonomic examination.

Thanks to the invaluable donation it has been possible for us to compare the specimens from Japanese waters with the type species of *Pinnaxodes* from Chile, *P.*

chilensis (H. Milne Edwards). Detailed comparison revealed that *Pinnaxodes major* Ortmann is congeneric with the type species, but *P. mutuensis* Sakai should be transferred to the genus *Holothuriophilus* Nauck, 1880, which had been long considered to be synonymous with *Pinnotheres* but was recently resurrected by Manning (1993a).

1. Taxonomic and ecological notes on *Pinnaxodes chilensis* (H. Milne Edwards, 1837)

The specimens at hand, 12 ovigerous females (12.7–18.9 mm in carapace breadth) and one non-ovigerous female (12.7 mm in carapace breadth), were obtained on 26 September 1997 from about 30 individuals of sea urchin, *Loxechinus albus*, purchased at the Fermondt Market, Santiago, Chile, which were collected at Isla Maillen by local fishermen. All of the crabs were found in the recta of sea urchins; the lumina were each filled with a big female crab.

Verrill (1869) considered that a crab grown in the rectum of a sea urchin eventually weakens or kills its host by irritation, based on the fact that nearly all the sea urchins found cast up on the beach, amounting to more than one hundred, had the crabs. It is not apparent from this observation whether the presence of such unwelcome occupants is immediately or slowly lethal for sea urchins or not, but it is certain that the crabs cause deformities in the shells of the host sea urchins, and also highly probable that the sufficient development and full reproductive ability are more or less obstructed in the host sea urchins. According to Verrill (1867a, b), a crab had effected a lodgment in the upper part of the intestine, which has thereby been greatly distended in the form of a membranous sac, attached to one side of the shell, and extending around to the lower surface near the mouth. The shell is usually swollen on the side over the sac, and the anal area is depressed and distorted, with a large open orifice passing obliquely into the sac, out of which the crab may thrust its legs. Thus, the crab is apparently unable to come entirely out.

Jackson (1912) also mentioned the presence of a crab in the rectum of *Loxechinus albus* and *Caenocentrotus* (=*Strongylocentrotus*) *gibbosus*, especially in the latter, of which nearly all the individuals examined by him were infected. According to him, the crab when small forces its way into the anus, dilating and deforming the rectum into a sac that may reach to the peristome and in which the crab sits with claws protruding. Verrill (1867a, b) had already noticed the remarkable frequency of parasitism, and later the high percentage, 97.6 %, was definitely demonstrated by Schwabe (1936), who found 121 crabs (107 females and 14 males) in 124 sea urchins from Isla Santa Maria, Chile. This means that almost all the sea urchins are each carrying a crab in the rectum.

The specimens at hand agree well with the descriptions and figures given by Rathbun (1918) and Garth (1946, 1957). The body is thick and high, and the carapace is strongly vaulted in both directions, with the width slightly greater than the

length, and subquadrate with dorsal surface ill-defined, smooth and polished; frontal and lateral margins are densely fringed with soft and long hairs (Fig. 1A). The frontal margin is narrow, straight and interrupted by a median shallow sulcus. The eyestalk is not completely embedded in the orbit, being partially visible in the dorsal view; the cornea is pigmented as a small dot. The third maxilliped is densely covered with long and extremely soft hairs like the frontal margin, and characteristic especially in the shape of the propodus and dactylus as figured by Heller (1865), Rathbun (1918), Garth (1957) and in the present paper (Fig. 2C); the dactylus is distinctly spatulated, articulated at the median part of the inner margin of the propodus, exceeding far beyond the tip of the propodus by more than its distal half; the distal half of the propodus is so obliquely truncated that the propodus and dactylus covering the buccal cavern in the natural position seem to be one segment as a whole which is obliquely cut into two; the ischium and merus are basically fused, but its suture line is always distinct on the outer surface. The second maxilliped (Fig. 2D) is stout and wide, with rounded dactylus. The chelipeds and ambulatory legs are comparatively thick and densely fringed with long and soft hairs that disguise the details of the margins.

Examining a small male (7.6 by 7 mm) from Port Otway, Chile, Rathbun (1898) considered that *Pinnaxodes hirtipes* Heller might be distinct from *P. chilensis* (H. Milne Edwards), but later, in Rathbun (1918), the identification was corrected, with short notes on variation. The full synonymy of *P. chilensis* is referred to in Schmitt *et al.* (1973).

This species ranges reliably from Ecuador southward to Port Otway (Puerto Barroso) in Chile, and also is known from the Galapagos Islands. In the preliminary biogeographic notes on the Argentine decapod crustaceans, Boschi (1966) checked the occurrence of this species in the column of cold-temperate region (lat. 51-56° S; region of Tierra del Fuego and the Magellan Straits). Fenucci (1967) also mentioned the southern limit as the west or Pacific side entrance to the Magellan Straits.

The host sea urchins are *Loxechinus albus* (Molina) (Rathbun, 1918; Schwabe, 1936; Garth, 1957; present paper) and *Strongylocentrotus gibbosus* (Agassiz) (Rathbun, 1918; Garth, 1946, 1957).

2. Systematic notes on the *Pinnaxodes* species

Manning (1993a) removed three genera, *Arcotheres* Bürger, *Holothuriophilus* Nauck and *Zaops* Rathbun, from the synonymy of the genus *Pinnotheres*, and in the revision of the subfamily Pinnotherinae from West Africa, Manning (1993b) established six new genera and made a non-dichotomous key for all the genera known to the date, 26, including the Indo-Pacific genera. According to these papers, 1) in *Arcotheres* and *Zaops* the ambulatory dactyli are unequal and dissimilar, differing from the subequal and similar dactyli in *Holothuriophilus* and *Pinnotheres*, 2) in *Holothuriophilus* the carapace is quadrangular, with the broadly spatulate dactylus of the third maxilliped, whilst the carapace is subhexagonal or subcircular in *Pinnotheres*,

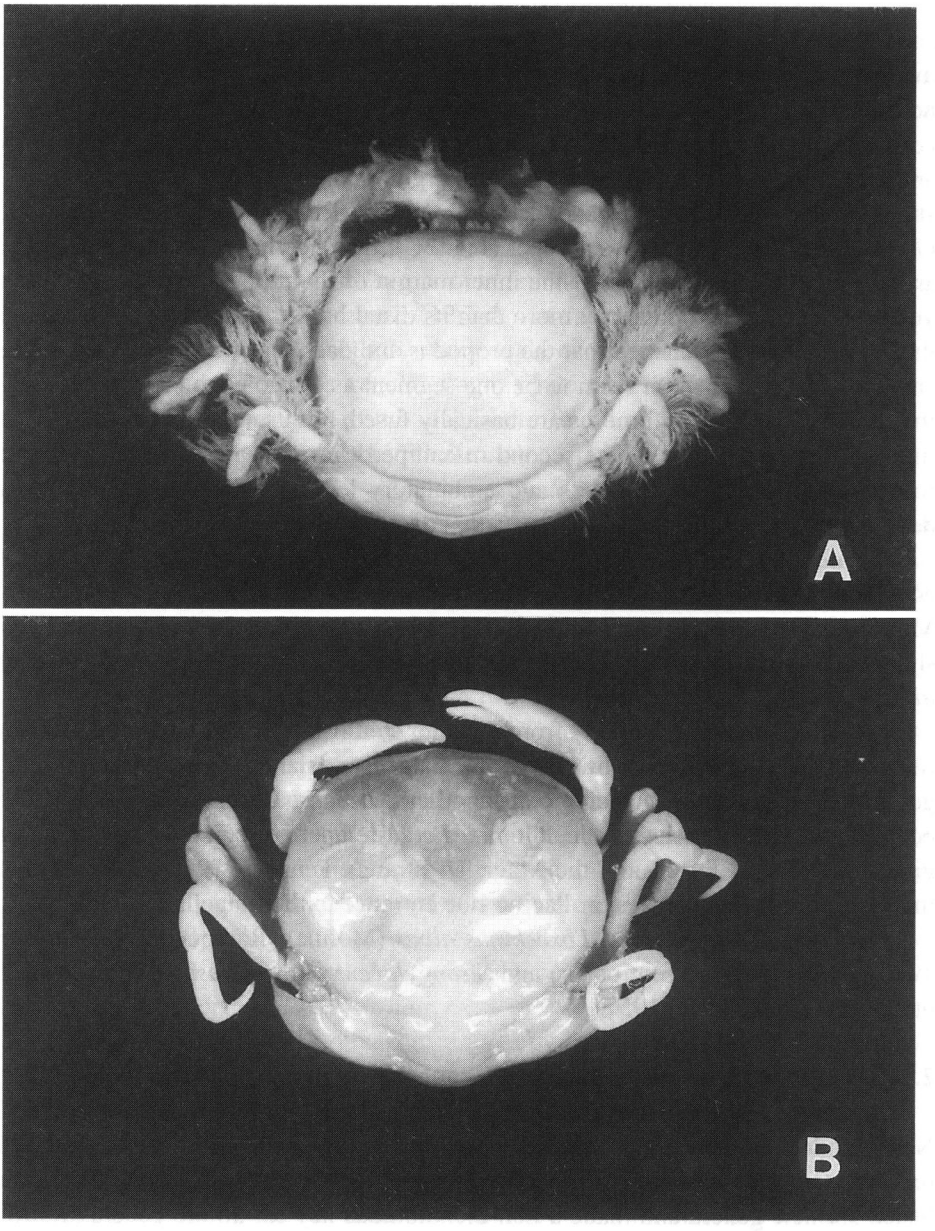

Fig. 1. A, *Pinnaxodes chilensis* (H. Milne Edwards), ovig. ♀ (NSMT; cb 15.0 mm). B, *Holothuriophilus mutuensis* (Sakai), comb. nov., ovig. ♀ (NSMT; cb 16.5 mm).

with the slender dactylus of the third maxilliped, and 3) *Pinnaxodes* is distinguished from the related genera by having the ischium and merus of the third maxilliped separated by a distinct suture. The most important distinguishing feature of *Pinnaxodes* is, therefore, in the structure of the third maxilliped, the ischium and merus of which are distinctly separated by a transverse suture. Otherwise, he mentioned that the members of *Pinnaxodes* and *Holothuriophilus* inhabit exclusively echinoids and holothurians, respectively. All of these reasons are not always keen, but the validity of these genera is acceptable.

In this paper the second and third maxillipeds of some species including *Pinnaxodes chilensis*, the type species of the genus, are figured for comparison and consideration of the generic validity (Fig. 2). In *Pinnotheres pholadis* de Haan (Fig. 2A), one of the commonest pinnotherid crabs living in bivalve shells from Japan, the ischium and merus of the third maxilliped are completely fused to form an elongate plate, with the inner margin being weakly concave along the whole length; the styliform dactylus does not exceed the tip of the propodus. In *Pinnaxodes chilensis* (Fig. 2C) and *P. major* (Fig. 2E), both segments in question are fused, but with a distinct suture on the outer surface, with the inner margin convex or rather angulated in the middle; the dactylus is distinctly spatulated and exceeds the tip of the propodus, especially in *P. chilensis*, as noted elsewhere. On the other hand, in *Pinnaxodes mutuensis* (Fig. 2G) both segments are completely fused, but the inner margin is strongly concave and constricted to show the original place of articulation; the dactylus is spatulated more distinctly than that of *Pinnotheres pholadis*, but less than those of the two *Pinnaxodes* species mentioned above.

The second maxillipeds (Fig. 2B, D, F, H) are specifically distinct from each other. The exopod is provided with a small notch in *Pinnotheres pholadis* (Fig. 2B) and *Pinnaxodes chilensis* (Fig. 2D), but it is apparent that the second maxilliped is not of sufficient morphological value to warrant generic status.

1) East Pacific species

As already mentioned, the type species of the genus *Pinnaxodes* is *P. chilensis* (H. Milne Edwards, 1837) ranging from Ecuador to the entrance of the Magellan Straits along the west coast of South America.

Pinnotheres silvestrii Nobili, 1901 was transferred to *Pinnaxodes* by Garth (1957), who has confirmed its identity as a senior synonym over *Pinnaxodes meinerti* Rathbun, 1904, and Manning (1993a) further synonymized *Pinnaxodes silvestrii* with *Holothuriophilus pacifica* (Poeppig, 1836). According to Garth (1957), *P. silvestrii*, now known as *H. pacifica*, is found in the cloaca of the holothurian, probably *Eucyclus chilensis* (Semper), and the fusion of the ischium and merus of the third maxilliped is essentially complete, with a superficial line of suture on the outer surface. *Holothuriophilus pacificus* from Chile is the southern counterpart of *H. trapeziformis* Nauck, 1880, the type species of *Holothuriophilus*.

Pinnaxodes gigas described by Green (1992) from Morro Colorado, Mexico

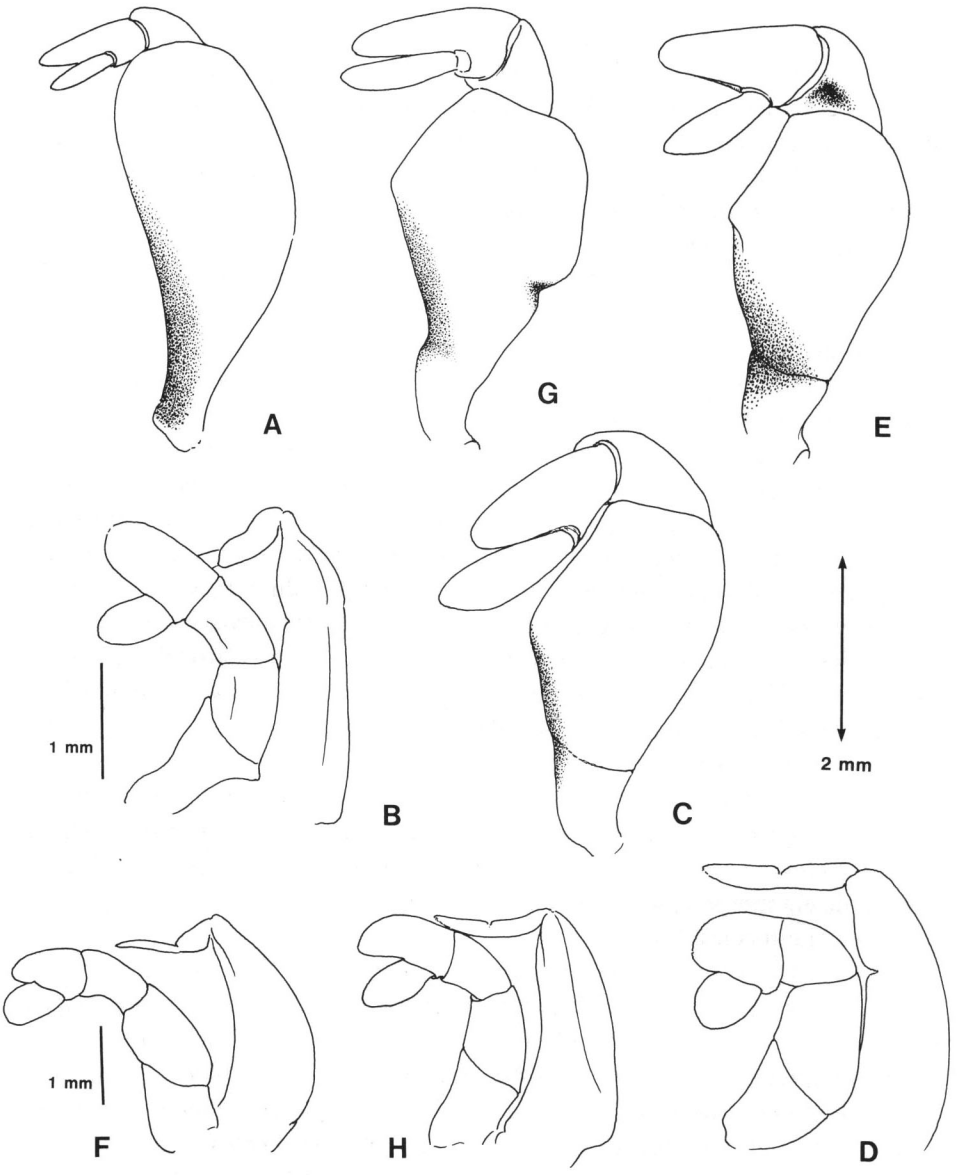

Fig. 2. Second (B, D, F. H) and third (A, C, E, G) maxillipeds, without exopods of third maxillipeds and marginal hairs. A, B, *Pinnotheres pholadis* de Haan, ♀ (NSMT-Cr 7325; cb 14.5 mm) from *Mytilus edulis* Linnaeus in Tokyo Bay. C, D, *Pinnaxodes chilensis* (H. Milne Edwards), ovig. ♀ (NSMT; cb 17.5 mm). E, F. *Pinnaxodes major* Ortmann, ♀ (NSMT; cb 16.5 mm). G, H, *Holothuriophilus mutuensis* (Sakai), comb. nov., ovig. ♀ (same individual as in Fig. 1B) (NSMT; cb 16.5 mm). Arrowheaded scale is applied to Figs. A, C-E, G, H.

was later recorded by Campos *et al.* (1998) from Bajo Macho in the upper Gulf of California, Mexico. This species is closely related to *P. floridensis* Wells et Wells from the West Atlantic commented in the next section. These two species are without doubt congeneric with each other and also with *P. chilensis*. Following Rathbun's comment (1918) that the genus *Opisthopus* Rathbun, 1893 of the subfamily Asthenognathinae, not of the Pinnotherinae, perhaps should be united with *Pinnaxodes*, Campos *et al.* (1998) also doubted the systematic validity of *Opisthopus*, which was established to accommodate the monotypic representative, *O. transversus* Rathbun, 1893. The genus *Opisthopus* may be maintained until the expected systematic revision of the species symbiotic with sea cucumbers, but in due course the change of its scientific name from *Opisthopus transversus* to *Pinnaxodes transversus* may be conceivably possible.

2) West Atlantic species

Pinnaxodes floridensis Wells et Wells, 1961 was fully described by the original authors, with excellent figures, on 174 specimens obtained from the cloaca and respiratory tree of the sea cucumber, *Theelothuria princeps* (Selenka). It is reasonable that the species is actually referred to *Pinnaxodes*, especially in view of the nature of the third maxilliped. The original authors made the important observation about the third maxilliped that in females the fusion between the ischium and merus is incomplete, a more or less distinct suture extending about two thirds across the breadth of the endognath, and also that in males this suture continues across the endognath, effecting a complete separation between the two segments. In the original description the new species was compared only with *P. chilensis* and *P. silvestrii*, the latter of which is now known as *Holothuriophilus pacificus*. In reality, however, it is much closer to *Pinnaxodes major* Ortmann from the West Pacific in the general shape of the carapace, chelipeds and ambulatory legs, as well as the third maxilliped, which is also found in the cloaca of sea cucumbers. The distal part of the first male pleopod is strongly curved outward almost at right angles to the shaft, differing from that of *P. major*, in which the distal part is more or less sickle-shaped, with a long inward-directed process at its apex, as figured by Sakai (1965). Nearly all that is known of this species is given by the original authors, but Williams (1984) recorded its distribution as from off North Carolina to Georgia and northwest Florida.

In the central West Atlantic the genus *Pinnaxodes* was represented by one more species, *P. tomentosus* Ortmann, 1894 from Brazil. *Pinnaxodes tomentosus*, which was considered by Rathbun (1918) to be very likely a species of *Pinnotheres*, is only poorly known; the original figures are not elaborate, but at least it is possible to mention that the dactylus of the third maxilliped is more or less spatulate, wider than the *Pinnnotheres*-type dactylus, placed side by side with the propodus, and does not exceed the tip of the propodus. The carapace is circular in its outline and covered with short soft felt, and the ambulatory legs are very slender. Its true systematic position may be in the genus *Holothuriophilus*, not in the genus *Pinnotheres*.

As a result, in the West Atlantic, the genus *Pinnaxodes* is represented only by *P. floridensis* Wells et Wells, and *Pinnaxodes tomentosus* Ortmann may be transferred to the genus *Holothuriophilus*, not to the genus *Pinnotheres*.

3) West Pacific species

The West Pacific representatives of the genus *Pinnaxodes* are *P. major* Ortmann, 1894 from Japan, Korea and the Russian Far East, and *P. mutuensis* Sakai, 1939 from northern Japan.

In Japanese waters *Pinnaxodes major* is rather well known due to the repeated contributions by Sakai (1939, 1965, 1976) with fine drawings, and also, at the Tokyo Market, it is often found in the mantle cavity of the edible bivalve shell, *Atrina pectinata* (Linnaeus), which had probably been collected at the shallow mud bottom of the Seto Inland Sea. During this study we examined the following specimens preserved in the National Science Museum, Tokyo (NSMT) and the Zoological Reference Collection, University of Singapore (ZRC).

Mimase, Tosa Bay, 2 young ♀♀ (NSMT-Cr 4400; cb 8.6×cl 7.5 mm, cb 9.0×cl 8.3 mm), Feb. 1974, Y. Koyama leg.

Tokyo Market, 1 ♀ (NSMT-Cr 3508; cb 22.0 mm), further data unknown; 4 ♀♀ (NSMT; cb 14.5–16.7 mm), 2 ♀♀ (ZRC; cb 13.5, 20.0 mm) from *Atrina pectinata* (Linnaeus), Feb. 3, 1999, M. Takeda & P. K. L. Ng leg.

In most of these specimens the carapace is rather hard and covered typically with a dense coat of soft tomentum, with regions ill-defined (Fig. 3A), but in some specimens the dorsal surface of the carapace is partly or sometimes nearly completely naked and shining (Fig. 3B). Each anterolateral margin of the carapace is arched to form a blunt shoulder in the middle and is more or less thick with marginal rim for the whole length, and thus the posterolateral margin behind the end of the anterolateral marginal rim is weakly concave subdorsally. The chelipeds and ambulatory legs are of a stout appearance, being covered with dense tomentum. In the subadult females from Tosa Bay, the carapace, chelipeds and ambulatory legs and even the third maxillipeds (Fig. 4C) are covered densely and uniformly with dark-colored setae rather than tomentum.

In addition, through the courtesy of Dr H. Namikawa of the Showa Memorial Institute, National Science Museum, Tokyo (SMI), we had a good chance to examine a male (SMI no. 3817; cb 9.0×cl 7.3 mm) from off Hayama, Sagami Bay collected by the late Showa Emperor of Japan, on 19 July 1959. This specimen was figured in dorsal view to depict the male character (Fig. 4A). The general shape of the carapace, chelipeds and ambulatory legs is somewhat similar to those of the young females from Tosa Bay, but the dorsal surface of the carapace is sparsely covered with tomentum, with the frontorbital region developed so as to be visible from above. The male abdomen (Fig. 4B) is seven-segmented, with a laterally expanded and distally angulated terminal segment.

Pinnaxodes mutuensis Sakai, 1939 is known only by the original description

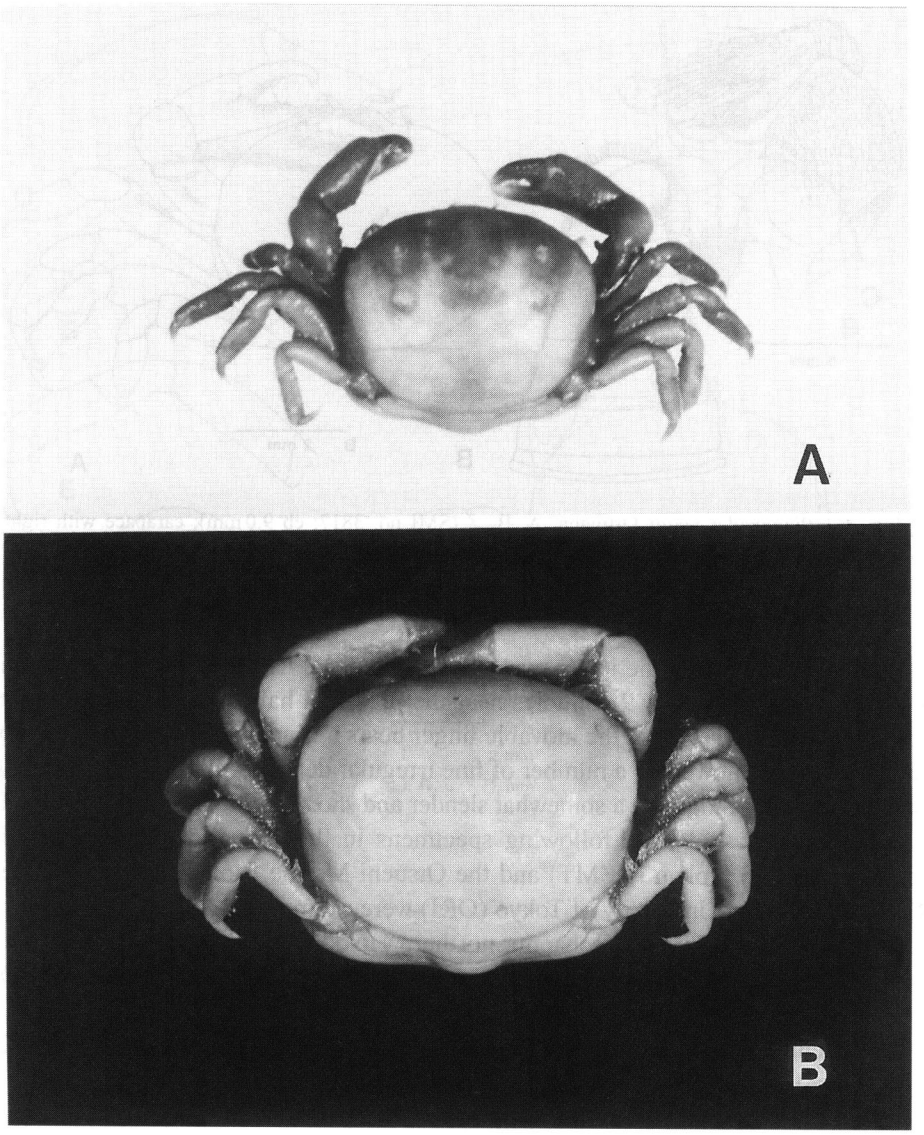

Fig. 3. *Pinnaxodes major* Ortmann. A, ♀(NSMT; cb 15.7 mm); B, ♀(NSMT; cb 18.3 mm).

based on 9 females and 1 male from Aomori Bay in northern Japan. Its host was the bivalve shell, probably *Modiolus modious* (Linneaus) (as *Volsella modiolus* by Sakai, 1939). The original description is not always thorough, but the carapace (Figs. 1B, 5A) is entirely naked, smooth and a rounded quadrangle in outline, with the lateral borders obscurely angulated in the middle; the chelipeds are also naked, but the palm

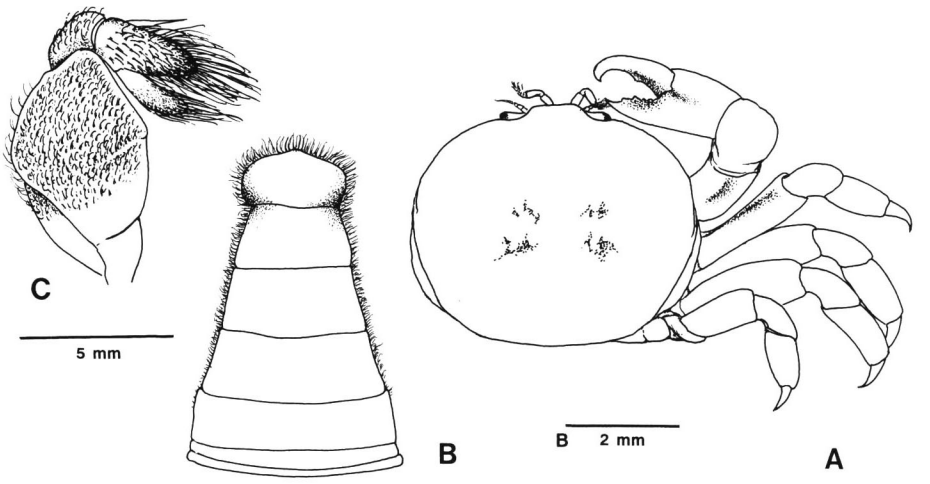

Fig. 4. *Pinnaxodes major* Ortmann. A, B, ♂ (SMI no. 3817; cb 9.0 mm); carapace with right cheliped and ambulatory legs (A) and abdomen (B). C, right third maxilliped of young ♀ (NSMT-Cr 4400; cb 8.6 mm).

is sparingly hairy along the lower margin near the distal half; the cutting edge of immovable finger bears 8 or 9 denticles near the proximal half, with the distal half entire, and the cutting edge of the movable finger bears a triangular tooth near the proximal end and is followed by a number of fine irregular denticles (Fig. 5C); the ambulatory legs are very thin, with a somewhat slender and short last pair (Figs. 1B, 5A, D-F).

During this study, the following specimens in the collections of the National Science Museum, Tokyo (NSMT) and the Otsuchi Marine Biological Center, Ocean Research Institute, University of Tokyo (ORI) were examined.

Soya Straits off Cape Noshappu, northern Hokkaido, 1 ♀ (cb 14.5 mm) and 12 ovig. ♀♀ (NSMT-Cr 11256; cb 14.5–17.5 mm) from *Crenomytilus grayanus* (Dunker), Feb. 25, 1991, T. Miyauchi leg.

Otsuchi Bay, Iwate Pref., northeastern Honshu, 5 ovig. ♀♀ (ORI; cb 10.5–22.0 mm), from *Mytilus gallprovincialis* Lamarck, Feb. 26, 1982; 4 ♂♂ (ORI; cb 5.0×cl 4.8−cb 7.0×cl 6.5 mm), 5 ovig. ♀♀ (ORI; cb 10.0–14.3 mm), May 19, 1982.

These specimens generally agree with the original description, although the contour of the carapace is somewhat variable. The carapace is usually more or less angulated as in the original figure (Fig. 5G, H), but in some specimens the lateral borders are very obscurely angulated or almost regularly convex without special angulation (Fig. 5A). In some specimens the posterior border of the carapace is convex outward weakly (Fig. 5G) or rather strongly (Fig. 5H).

The general appearance of this species is just like the *Pinnotheres* species, hav-

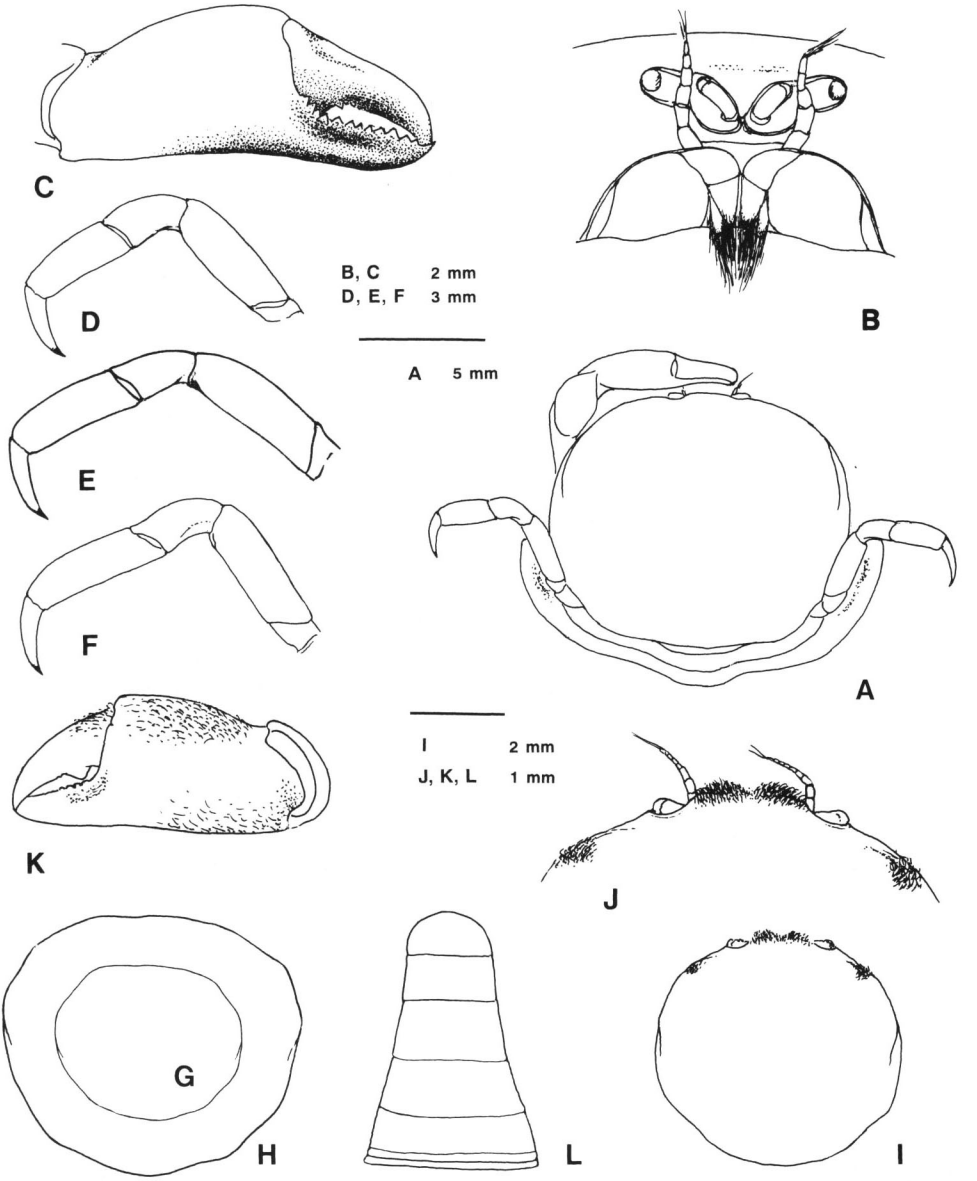

Fig. 5. *Holothuriophilus mutuensis* (Sakai), comb. nov. A–F, ♀ (ORI; cb 11.0 mm); dorsal and frontal views (A, B), right chela (C), left first to third ambulatory legs (D–F). G, H, ♀♀ (NSMT; cb 17.0, 16.6 mm) showing contour of carapaces. I–L, ♂ (ORI; cb 4.8 mm); carapace (I), frontorbital region (J), left chela (K), abdomen (L).

ing a soft naked carapace and slender ambulatory legs, but the dactylus of the third maxilliped is spoon-shaped and a good deal exceeding the tip of the propodus (Figs. 2G, 5B). The fusion of the ischium-merus of the third maxilliped was not mentioned in the original description; it is essentially complete, and a quite imperfect suture may be traceable only on the external surface under special light control.

The male is small and also of similar appearance to the *Pinnotheres* males; the carapace (Fig. 5I) is subcircular, with the protruded frontal region, evenly convex in both directions, hard and smooth; the anterolateral margin is, however, weakly ridged somewhat like in the female and provided with a small area covered with setae (Fig. 5I); the frontal marginal and submarginal regions are also covered with setae (Fig. 5J); the movable finger is armed with a strong conical tooth near the base (Fig. 5K); the ambulatory legs are slender, with a row of long feathered hairs; the abdomen is seven-segmented, with the terminal segment not expanded (Fig. 5L); the first pleopod is weakly curved outward for its whole length, with some subterminal long hairs, tapering toward the tip; the third maxilliped is quite similar to that of the female.

Based on the nature of the third maxilliped, it is concluded that *Pinnaxodes major* is retained in the genus *Pinnaxodes*, but *P. mutuensis* is transferred to the genus *Holothuriophilus*.

The type locality of *Pinnaxodes major* is Tokyo Bay, and then this species is, as the full synonymies given by Schmitt *et al.* (1973), recorded from Vladivostok and Cape Solotei (Sufren) (=Gulf of Tartary) , U.S.S.R. by Balss (1922), Mutsu Bay by Yokoya (1928), Seto (=Shirahama), Ise Bay and Tateyama Bay by Sakai (1939), some localities in Sakhalin by Urita (1942), S. E. Siberia, Sakhalin and S. Kuriles by Kobjakova (1967), Sagami Bay by Sakai (1965), and Korea (Kim, 1973). Although it is difficult to confirm at present, the records of *P. major* by Balss (1922), Yokoya (1928) and Urita (1942) are probably due to misidentification of *Pinnaxodes mutuensis*, which should be known as a species of *Holothuriophilus*.

The host of *P. major* is the sea cucumber found in shoal waters, *Holothuria decorata* von Marenzeller (as *H. monacaria* by Sakai, 1939), and the bivalve shell stuck in the shallow-water mud bottom, *Atrina pectinata* (Linnaeus) recorded in this paper.

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