

**On two new genera of pea crabs parasitic in holothurians
(Crustacea: Decapoda: Brachyura: Pinnotheridae) from the
Indo-West Pacific, with notes on allied genera**

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Abstract.—Two new genera of pea crabs of the family Pinnotheridae, *Holotheres* and *Buergeres*, members of which are parasites of sea cucumbers, are described from the Indo-West Pacific. Species of *Holotheres* are characterized by having all the dactyli of the walking legs of females short and subequal in length, with the spatuliform dactylus of the third maxilliped inserted very near or at the base of the propodus. Species of *Buergeres* are characterized by having the last dactyli of the walking legs of females elongate and longer than those of the other legs, with the subspatuliform dactylus of the third maxilliped inserted distinctly before the base of the propodus. *Holotheres* and *Buergeres* are compared to other genera whose members are associated with holothurians, *Holothuriophilus* Nauck, 1880, and *Alain* Manning, 1998 (obligate parasites); as well as *Pinnaxodes* Heller, 1865 (facultative parasites).

In a synopsis of the Pinnotheridae, Manning (1993a: 127, 128) defined the genus *Pinnotheres* Bosc, 1802, sensu stricto as having a subhexagonal or subcircular carapace without any surface ornamentation or sculptures, a third maxilliped which has the ischium and merus completely fused (without any trace of a suture) and a three-segmented palp in which the dactylus is slender, inserted basally on the propodus; the dactyli of the first to fourth walking legs are subequal and similar, short and strongly curved, with the tips simple; and all the seven male abdominal somites are free. Manning (1993a), however, did not treat most of the species of *Pinnotheres* which live in holothurians, all of which have a third maxilliped in which the dactylus is not slender but spatuliform to subspatuliform.

In addition, the third maxilliped of most of these species has the inner margin usually angular, and the carpus of the third maxilliped is distinctly shorter than the propodus that is relatively long and slender. In this combination of characters, these species are very different from almost all other taxa now classified in *Pinnotheres* sensu stricto or any of the other non-holothurian symbiotic genera recognized or described by Manning (1993a, 1993b) and other workers. Manning (1993a:128) did note briefly in his synopsis, however, that one genus parasitic in holothurians, *Holothuriophilus* Nauck, 1880, was valid, and subsequently elaborated more on this (Manning 1993b).

Currently, 16 species of pinnotherid crabs are known to be parasites of holothurians, and of these, 13 occur only in the Indo-West Pacific (see Schmitt et al. 1973, Hamel et al. 1999). The eastern Pacific spe-

* Deceased 18 January 2000.

cies which are obligate parasites in holothurians are both members of *Holothurionophilus* Nauck, 1880, although one species of *Opisthopus* Rathbun, 1893, is occasionally found in sea cucumbers (Rathbun 1918, Schmitt et al. 1973). The 13 Indo-West Pacific species are *Alain crosnieri* Manning, 1998 (Indonesia); *Ostracotheres holothuriensis* (Baker, 1907) (South Australia); *Pinnaxodes major* (Ortmann, 1894) (Japan); *Pinnotheres deccanensis* Chopra, 1931 (southern India); *P. flavus* Nauck, 1880 (Philippines); *P. halingi* Hamel, Ng & Mercier, 1999 (Solomon Islands); *P. holothuriae* Semper, 1880 (Philippines); *P. ortmanni* Bürger, 1895 (Philippines, Peninsular Malaysia, Singapore); *P. pilumnoides* Nobili, 1905 (Red Sea, Gulf of Aden); *P. semperi* Bürger, 1895 (Java, Sumatra, Sulawesi, Singapore); *P. setnai* Chopra, 1931 (Andaman Islands); *P. tenuipes* Bürger, 1895 (Philippines); and *P. villosissimus* Doflein, 1904 (Sumatra, Andaman Islands, New Guinea) (Chopra 1931, Schmitt et al. 1973, Pregonzer 1988, Van den Spiegel & Jangoux 1989, Hamel et al. 1999).

Most of the species parasitic in holothurians now placed in *Pinnotheres* sensu lato can, however, be divided into two distinct "groups" on the basis of the dactyli of their walking legs and form of the third maxilliped (see Hamel et al. 1999). Members of one "group" (*P. semperi*, *P. flavus*, *P. villosissimus* and *P. setnai*) have all the dactyli of the female walking legs short and similar in length, and the dactylus of the palp of the third maxilliped inserted at the base of the propodus. Members of the second "group" (*P. ortmanni*, *P. holothuriae*, *P. tenuipes* and *P. deccanensis*) have the dactyli of the last female walking leg styliform and much longer than the short and hooked dactyli of the other three pairs of legs, and the dactylus of the palp of the third maxilliped inserted well before the base of the propodus.

The present paper serves to diagnose two new genera for these two "groups". The abbreviations MXP3 refers to the third

maxilliped; WL1-4 refer to the first to fourth walking legs respectively; and G1 to the male first pleopod. The terminology follows Manning (1993a). Measurements are of the carapace width and length, respectively. Specimens examined are deposited in the Zoological Reference Collection of the Raffles Museum, National University of Singapore (ZRC); Senckenberg Museum, Frankfurt-am-Main (SMF); National Science Museum, Tokyo (NSMT); Zoological Museum of the University of Copenhagen (ZMUC); and National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Notes on the Material of Otto Bürger

A note on the pinnotherid material of Semper, Nauck and Bürger in the USNM is necessary. In 1906, the USNM received six lots of pinnotherid crabs on exchange from the University of Göttingen in Germany. This material was from the collections made by C. Semper and was used for several studies by Semper (1880), Nauck (1880) and Bürger (1895), all of whom were at the University of Göttingen. All of this material was reported by Bürger (1895). This shipment included: *Pinnotheres affinis* Bürger, 1895 (1 ovigerous female, 9.5 by 8.2 mm, Bohol, Philippines, USNM 32435); *Pinnotheres exiguus* Bürger, 1895 (1 ovigerous female, 5.6 by 4.6 mm, Samar, Philippines, USNM 32432); *Pinnotheres flavus* Nauck, 1880 (2 ovigerous females, 8.4 by 7.8 mm, 10.0 by 9.5 mm, Zamboanga, Philippines, USNM 32434); *Pinnotheres glaber* Bürger, 1895 (1 ovigerous female, 7.8 by 6.5 mm, Palawan Island, Palaos Islands, USNM 32431); *Pinnotheres holothuriae* Semper, 1880 (2 ovigerous females, 10.1 by 9.3 mm, 8.0 by 6.5 mm, Zamboanga, Philippines, USNM 32433); and *Xenophthalmus latifrons* Bürger, 1895 (1 ovigerous female, 9.5 by 8.1 mm, Bohol, Philippines, USNM 32436).

Mary Jane Rathbun, then Second Assistant Curator of Invertebrates at the USNM,

considered these specimens to be types. Checking with various museums, including the collections in the University of Göttingen, Schmitt et al. (1973) tracked down many of the specimens of Semper, Nauck and Bürger but commented that the types of *P. exiguus*, *P. flavus*, *P. holothuriae* and *X. latifrons* were lost or unknown. Curiously, Schmitt did not check his own collections at the USNM. Apparently, sometime after 1906, at least some of Semper's material was transferred to the Zoological Museum, Berlin, where the true types of *P. affinis* and *P. glaber* are still extant (O. Coleman, in litt.). There are no types of *P. exiguus*, *P. flavus*, *P. holothuriae* and *X. latifrons* in the Berlin Museum (O. Coleman, in litt.). The surviving specimens, representing the bulk of Semper's material in the University of Göttingen, were recently transferred to the Senckenberg Museum. Michael Türkay and Andreas Allspach kindly provided a list of the extant Göttingen pinnotherid specimens now in the SMF. Of the species reported from holothurians by Semper, Nauck and Bürger, only specimens of two species are still extant, *P. flavus* and *Holothuriophilus trapeziformis*. There were also several lots in which the labels have been lost, but examination of this material by one of us (PKLN) did not uncover specimens of any pinnotherid species parasitic in holothurians. On the basis of this material, we also provide herein figures of *P. flavus* and *P. holothuriae*, each of which are transferred to one of the two new genera here recognized.

Taxonomic Account

Holotheres, new genus

Type species.—*Pinnotheres semperi* Bürger, 1895, by present designation.

Included species.—Five: *H. flavus* (Nauck, 1880), *H. halingi* (Hamel, Ng & Mercier, 1999), *H. semperi* (Bürger, 1895), *H. setnai* (Chopra, 1931), and *H. villosissimus* (Doflein, 1904).

Diagnosis.—Obligate symbionts in ho-

lothurians. Carapace circular to subcircular, often highly setose; posterior carapace margin distinctly convex. WL subequal right and left; WL3 similar in length, longer than WL4; female WL1–4 with dactyli short, similar in length and form. Ischium and merus of MXP3 completely fused, without trace of suture; dactylus of palp spatuliform, subequal in length to propodus, inserted near base of propodus. G1 simple, curved tube, tapering from base to tip, slightly recurved distally.

Etymology.—The name is derived from an arbitrary combination of the name for sea cucumbers *Holothuria*, and *Pinnotheres*. Gender masculine.

Remarks.—Among taxa wholly symbiotic with holothurians, *Holotheres* is perhaps closest to *Holothuriophilus* Nauck, 1880, sensu Manning, 1993b (type species *Holothuriophilus trapeziformis* Nauck, 1880). The dactylus and propodus of the palp of MXP3 of *Holothuriophilus* species (Fig. 7C), however, is distinctly shorter than those of *Holotheres* species (Figs. 1B, 3B). In any case, *Holothuriophilus* is known only for certain from the eastern Pacific (Manning 1993b). Takeda & Prince Masahito (2000) transferred *Pinnaxodes mutuenensis* (Sakai, 1939), which is known only from bivalves, to *Holothuriophilus* but we do not agree (see "Notes on *Pinnaxodes* and *Holothuriophilus*").

Two other genera, *Pinnaxodes* Heller, 1865, and *Opisthopus* Rathbun, 1893, have some species which are facultatively found in holothurians (Rathbun 1918, Schmitt et al. 1973), and have carapaces and MXP3 similar to those of *Holotheres*. Species of *Holotheres* can be easily separated from *Pinnaxodes* in having the posterior carapace margin prominently convex (Figs. 1A, J, 2A, 3A) (versus slightly convex to almost straight, Fig. 6A, E), a proportionally longer dactylus and propodus of the MXP3 (Figs. 1B, 3B versus Fig. 6B, F), the dactylus of the MXP3 is inserted near the base of the propodus (Figs. 1B, 3B) (versus inserted $\frac{1}{3}$ from base of propodus) (Fig. 6B,

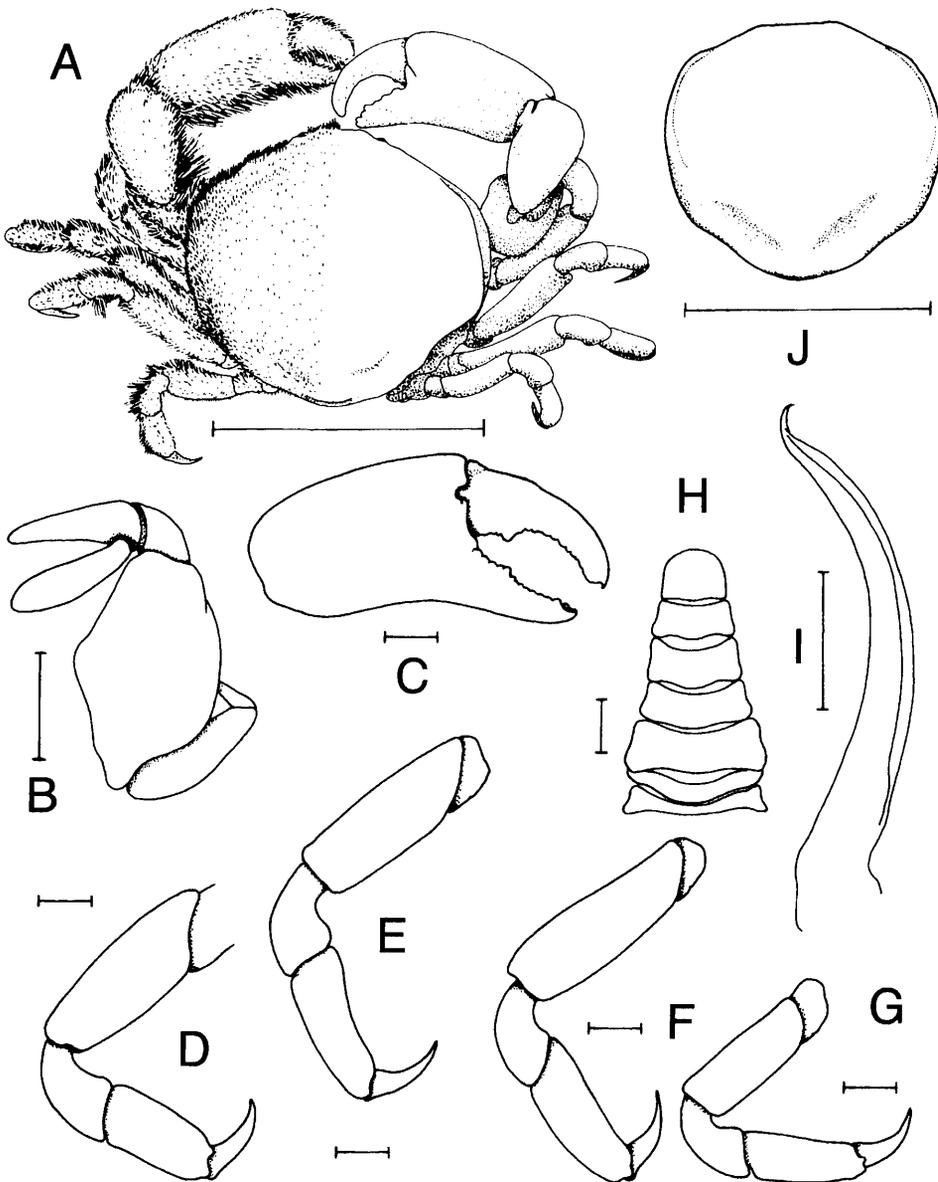


Fig. 1. *Holotheres semperi* (Bürger, 1895). A–I, neotype male (7.9 by 7.2 mm) (ZRC 1965.11.24.40); J, female (10.7 by 10.2 mm) (ZRC 1965.11.24.41). A, overall view of specimen (setae on right half of body denuded); B, left MXP3, outer view; C, right chela, outer view; D, WL1; E, WL2; F, WL3; G, WL4; H, male abdomen; I, left G1; J, carapace, dorsal view. (Except for A, all structures denuded.) Scales: A, J = 5.0 mm, B–I = 1.0 mm.

F), the ischium and merus are completely fused without any trace of a suture (Figs. 1B, 3B versus Fig. 6B, F), and the male telson is semicircular (Figs. 1H, 2G) (versus usually medially expanded laterally to form rounded to subpentagonal structure, cf.

Campos et al. 1998: fig. 3A, C; Takeda & Masahito 2000: fig. 4B) (see also Campos et al. 1998, Takeda & Prince Masahito 2000). *Opisthopus* has the same male abdomen form as *Holotheres*, but can be separated by the same carapace and MXP3

characters discussed above for *Pinnaxodes* (see Campos et al. 1998, Campos & Manning 2000).

Of the five species here included in *Holotheres*, the types of two species, *H. semperi* (Bürger, 1895) and *H. flavus* (Nauck, 1880), are considered to be lost. The taxonomy of only *H. semperi* and *H. flavus* are discussed herein. *Holotheres setnai* has been well described and figured by Chopra (1931). *Holotheres halangi* has been described and figured in detail by Hamel et al. (1999). *Holotheres villosissimus* (see Doflein 1904, Van den Spiegel & Jangoux 1989) is not well known and must be re-described when fresh specimens become available.

Holotheres semperi (Bürger, 1895)

Fig. 1

Pinnotheres semperi Bürger, 1895:382, pl. 9 fig. 28, pl. 10 fig. 27.—Lanchester, 1900:761.—Chuang, 1961:189, pl. 94.—Schmitt et al., 1973:85. (See Schmitt et al. (1973:85) for additional references).

Neotype.—Male (7.9 by 7.2 mm) (ZRC 1965.11.24.40) in respiratory tree of *Holothuria scabra*, coll. S. H. Chuang, 1950s.

Other material examined.—1 female (10.7 by 10.2 mm) (ZRC 1965.11.24.41), same data as neotype. 1 male (10.5 by 10.0 mm), 1 female (4.8 by 4.3 mm) (ZRC 1965.11.24.38–39), in cloaca of *Holothuria scabra*, coll. S. H. Chuang, 1950s. 2 males (7.7 by 6.8 mm, 7.0 by 6.6 mm), 2 females (11.2 by 9. mm, 10.7 by 9.0 mm) (all specimens badly damaged and carapace crushed in parts) (ZRC 1965.11.24.34–37), in cloaca of *Holothuria scabra*, coll. S. H. Chuang, 1950s. 1 male (8.4 by 7.9 mm) (ZRC 1965.11.24.16), 6–12 fathoms, from sea cucumber, Pulau Tekong, Singapore, coll. M. W. F. Tweedie, 1960s.

Diagnosis.—Male carapace subquadrate, width to length ratio ca. 1.1; female carapace subcircular, width length ratio 1.1–1.2; dorsal surface gently convex, covered with dense layer of short setae longer along lat-

eral regions, completely obscuring outline and surface; intestinal region slightly depressed. Anterolateral margin of male almost straight, lateral margin gently convex, posterolateral margin gently concave; anterolateral and lateral margin of female more confluent, gently convex; sub-branchial surface densely setose. MXP3 with ischium and merus completely fused, without trace of suture, subovate, inner margin subangular submedially; exopod relatively stout, outer margin convex, with well developed setae on flagellum; palp 3-segmented, propodus elongate, conical, subequal in length to dactylus; dactylus spatuliform, articulates at base of propodus. Chelipeds subequal; surfaces of merus, carpus, palm and fingers densely covered with setae, those on inner surfaces relatively longer; palm relatively stout; fingers shorter than palm; cutting edges of dactylus and propodus each with sub-basal large tooth and numerous denticles before and after it; distalmost part of fingers excavated on inner surface. WL relatively stout, WL2 > WL3 > WL1 > WL4 in length (basis-ischium to tip of dactylus); dactyli of WL1–4 relatively long, sharply tapering, all subequal in length; dorsal and ventral margins of meri, carpi and propodi of all legs densely lined with setae of various lengths, completely obscuring margins. Male abdomen with all 6 segments distinct, freely articulating, telson semicircular; lateral margins of segments 3–6 gently concave. Female abdomen with all segments freely articulating. G1 relatively slender, gently sinuous, tip distinctly curving upwards.

Biology.—*Holotheres semperi* has been reported from inside *Holothuria fursocinerea* and *H. scabra* (see Schmitt et al. 1973).

Remarks.—The identity of *Pinnotheres semperi* Bürger, 1895, is a problem. In describing the species on the basis of one male and one female, Bürger (1895:382, pl. 9 fig. 28, pl. 10 fig. 27) described and figured a female specimen with a subhexagonal carapace highly setose over its carapace and legs, well produced triangular frontal

margin, WL4 substantially shorter than the rest of the legs, and MXP3 in which the dactylus of the palp is spatuliform and as long as the propodus. A pair of specimens was subsequently reported by Lanchester (1900:761) who noted: "The specimens which Dr. Bürger has described came from the cloaca of *Hol. fusco-cinerea*; whereas the specimens we obtained from that Holothurian are, I find, referable to *P. ortmani*. The host, from which came Dr. Bürger's example of the latter species, was, I suppose, not known, as he makes no reference to it. In both these species, the animal was found high in the respiratory tree, forming an enormous gall; whether it would be able to extricate itself from this, and move, at will, up or down the respiratory tree, I do not know, but it has the appearance of a fixture, *nolens volens*". The species was next reported by Chuang (1961:189) who noted that the species occurs in the respiratory tree of the sea cucumber, *Holothuria scabra*: "A pair of them consisting of a male and a female may occur in one single sea cucumber. The relatively thick carapace, about 1 cm in diameter, is white in colour and has a circular outline. The cylindrical legs and both chelipeds are hairy".

In their synopsis of the Pinnotheridae, Schmitt et al. (1973) stated that the male and female syntypes of *H. semperi* (museum number not stated), which were originally in the University of Göttingen, are no longer extant. The Göttingen material, as discussed earlier, was examined by one of us (PKLN), and it does not contain any specimens which can be identified with this species. A check with the Berlin Museum confirms that the types of *H. semperi* are not there (O. Coleman, in litt.). They are also not in the USNM, and are thus almost certainly lost.

Comparisons of the present series of specimens from Singapore and the description and figures of the types by Bürger (1895), however, reveal a number of discrepancies. The relatively prominently produced triangular frontal margin of the fe-

male figured by Bürger (1895: pl. 9 fig. 28a) is an important one. The females on hand all have very narrow, non-protruding front, with the margin distinctly sinuous, and the eyes are not visible in dorsal view (Fig. 1J). In contrast, males have a more produced front, appearing subtruncate when viewed dorsally (Fig. 1A). Even when a specimen is angled such that the anterior part of the carapace arches upwards, the frontal margin never appears triangular. The frontal margins of uncleaned male specimens, however, are densely lined with setae and when covered with fine sediment, the "front" does appear to be more triangular in shape, especially when observed dry and the setae clump medially. None of the examined female specimens, however, resemble the specimen figured by Bürger, even when they are not cleaned. It would thus appear that Bürger might have figured an uncleaned, undenuded male rather than a female. It is also pertinent to note that the carapace shapes of the present males agree well with Bürger's figure, although the present specimens do not appear to be as setose. The distinct pattern of setae figured by Bürger is certainly not at all apparent in the present specimens. Bürger (1895:382) noted that the male he had, measured 7.0 mm by 6.8 mm, and the female 6.5 by 6.5 mm. All the present specimens examined are broader than long. Lanchester (1900:761), however, reported that his specimens were longer than broad (male 10.5 by 11.0 mm, female 7.75 by 8.0 mm). Whether these measurements were accurate or if they were taken from cleaned specimens could not be ascertained. The very short WL4 is noteworthy, as none of the present specimens on hand (male or female) has such a short WL4 as figured by Bürger (1895: pl. 9 fig. 28a). It seems likely though, that the WL4 of Bürger's specimen appears shorter than it actually is because the leg was bent slightly upwards when it was drawn. The MXP3 figured by Bürger (1895: pl. 10 fig. 27) agrees well with those of the present specimens, although the dactylus of the

palp he figured appears slightly less spatuliform, the dactylus is subequal in length to the propodus, and the outer margin of the fused ischium-merus is more rounded. The figure, however, is too schematic. The male abdomen figured by Bürger (1895: pl. 9 fig. 28b) is also too schematic to be of much use, although its general shape and proportions agree with those of the present specimens.

In describing *H. setnai* from the Andaman Islands (as *Pinnotheres setnai*), Chopra (1931:313) commented that his species differed from *H. semperi* in the carapace being more arched; the front is truncate with the anterior margin of the front depressed medially (not triangular); the large chela is more slender, with the palm proportionately longer and the fingers having well developed teeth; WL4 is very much smaller than the others; and the propodus of the palp of MXP3 is longer than the dactylus (not subequal in length). Of the above differences, as has been discussed earlier, only the proportions of the chela are really valid. On the basis of Chopra's (1931) excellent description and figures, it is clear that *H. setnai* and *H. semperi* are very close. Chopra, however, did not figure the carapace of the male. On the basis of Chopra's (1931) figures, *H. setnai* can also be separated from *H. semperi* by the relatively broader and more sinuous female frontal margin, the more slender ischio-merus of MXP3, and the carpus of the chelipeds not possessing a deep longitudinal cleft. Both species should thus be regarded as separate for the time being.

The pair of specimens figured by Chuang (1961: pl. 94: Figs. 2 and 3) is now in the ZRC (ZRC 1965.11.24.40-41), and the male, 7.9 by 7.2 mm (ZRC 1965.11.24.40), is here designated as the neotype of *Pinnotheres semperi* Bürger, 1895. The specimens are very consistent in all the characters discussed here. Other than the sexually dimorphic features of the abdomen and reproductive structures, the only major difference is in the shape of the carapace, be-

ing more ovate in the female (Fig. 1A versus Fig. 1J). The form and proportions of the chela and WL1-4 are not sexually dimorphic.

Holotheres flavus (Nauck, 1880)

Figs. 2, 3

Pinnotheres flavus Nauck, 1880:23, 66.—Bürger, 1895:383, pl. 9 fig. 29, pl. 10 fig. 29, 35.—Schmitt et al., 1973:45. (See Schmitt et al. (1973:45) for additional references).

Lectotype.—Male (8.6 by 7.9 mm) (SMF 951a), Bohol, Ubay, Philippines, coll. C. Semper, 1863-1864.

Paralectotypes.—2 males (7.9 by 7.6 mm, 8.0 by 7.6 mm), 2 females (10.3 by 10.0 mm, 8.9 by 8.0 mm) (SMF 951b), same data as lectotype. 2 ovigerous females (10.0 by 9.5 mm, 8.4 by 7.8 mm) (USNM 32434), Zamboanga, Philippines, coll. C. Semper, 1876.

Diagnosis.—Female carapace subcircular, width to length ratio ca. 1.1; female carapace subcircular, width length ratio ca. 1.1; dorsal surface gently convex, covered with short setae which obscures outline. Anterolateral margin arcuate, posterolateral margin gently convex; sub-branchial surface setose. MXP3 with ischium and merus completely fused, without trace of suture, subovate, inner margin subangular submedially; exopod relatively stout, outer margin convex, with well developed flagellar setae; palp 3-segmented, propodus elongate, subconical, subequal in length to dactylus; dactylus spatuliform, articulates at base of propodus. Chelipeds subequal; inner surfaces of merus, carpus, palm and fingers covered with setae; palm relatively stout; fingers shorter than palm; cutting edges of dactylus and propodus each with sub-basal large tooth and several denticles before it. WL relatively stout, WL2 > WL3 > WL1 > WL4 in length (basis-ischium to tip of dactylus); dactyli of WL1-4 relatively long, sharply tapering, all subequal in length; dorsal and ventral margins of meri, carpi

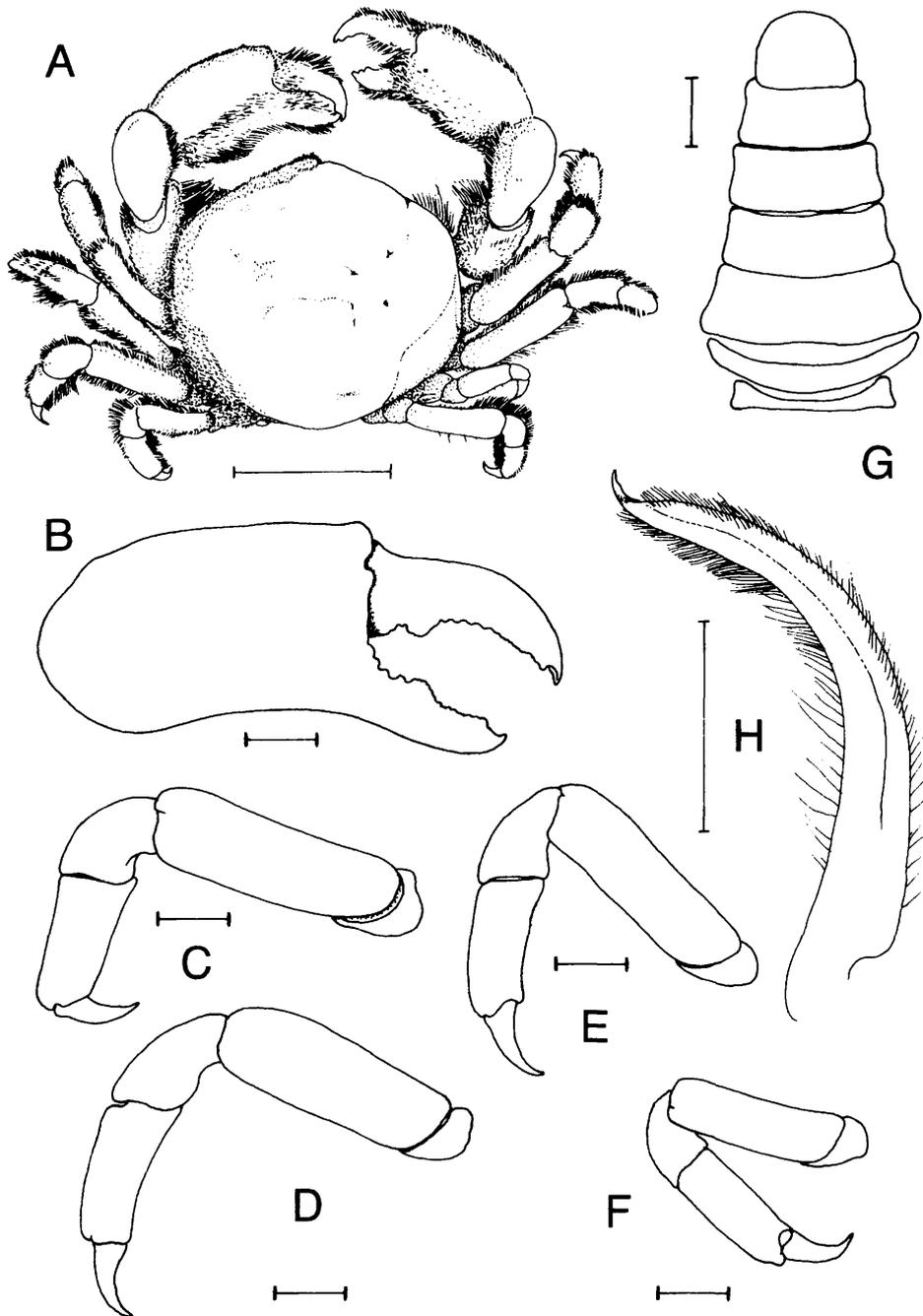


Fig. 2. *Holotheres flavus* (Nauck, 1880). Lectotype male (8.6 by 7.9 mm) (SMF 951a). A, overall view of specimen (setae on right half of body denuded); B, right chela, outer view; C–F, WL1–4 respectively; G, male abdomen; H, left G1. (Except for A, H, all other structures denuded.) Scales: A = 5.0 mm, B–H = 1.0 mm.

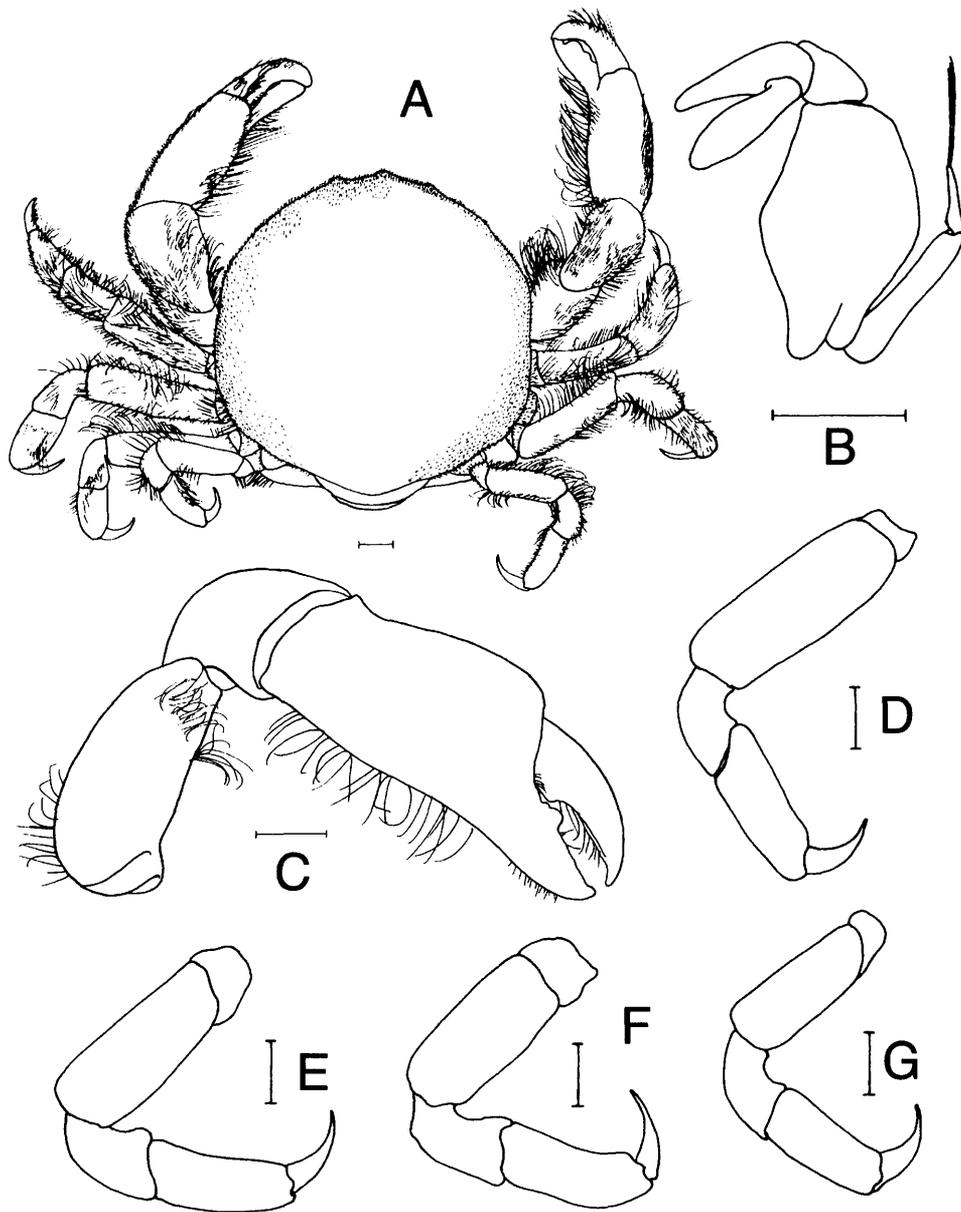


Fig. 3. *Holotheres flavus* (Nauck, 1880). Paralectotype female (10.0 by 9.5 mm) (USNM 32434). A, overall view of specimen; B, left MXP3 (denuded), outer view; C, right cheliped, outer view; D-G, WL1-4 respectively, denuded. Scales = 1.0 mm.

and propodi of all legs lined with setae of various lengths, obscures margins. Female abdomen with all segments freely articulating.

Biology.—Bürger (1895) noted that the species was collected from an unidentified holothurian. Nothing else is known.

Remarks.—*Holotheres flavus* was originally described by Nauck (1880) (as *Pinnotheres flavus*) on the basis of an unknown number of specimens from an unspecified site or sites in the Philippines, obtained from collections there by Semper (Nauck, 1880:5), although he did not

explicitly state so when describing the species. Bürger (1895:383) subsequently reported six males and six females collected by Semper from Zamboanga in the Philippines. De Man (1887:720, 721), who reappraised Nauck's taxa, provided measurements for only one male and one female (without specific location), suggesting he only had two specimens. Schmitt et al. (1973:45) commented that there were "2 syntypes: ZIMB 67/297 [Göttingen Museum], no longer extant; type locality: 'Philippinen'". How Schmitt et al. (1973) knew there were only two syntypes was not stated, perhaps these were the specimens used by De Man (1887). As discussed earlier, two of the females from Göttingen were actually given to the USNM, and the SMF has taken over from Göttingen three male and two female specimens of *P. flavus*. There are no specimens on this species in the Berlin Museum (O. Coleman, in litt.). Since Semper's material was used by Nauck, Bürger and De Man, it is reasonable to believe that all the material on hand are syntypes. We hereby select a male (8.6 by 7.9 mm, SMF 951a) as the lectotype of *Pinnotheres flavus* Nauck, 1880.

Holotheres flavus is similar to *H. semperi*, but can be distinguished by its more quadrate male carapace with the lateral margins straighter, appearing subparallel (Fig. 2A) (versus more rounded, Fig. 1A), the dorsal surface of the carapace covered with pubescence only along the margins (Fig. 2A) (versus uniformly all over, Fig. 1A), and most significantly, the G1 is more strongly curved, appearing distinctly C-shaped (Fig. 2H versus Fig. 1I).

Buergeres, new genus

Type species.—*Pinnotheres ortmanni* Bürger, 1895, by present designation.

Included species.—Four: *B. deccanensis* (Chopra, 1931), *B. holothuriae* (Semper, 1880), *B. ortmanni* (Bürger, 1895), and *B. tenuipes* (Bürger, 1895).

Diagnosis.—Obligate symbionts in holothurians. Carapace circular to subcircular, broader than long. WL subequal right and left; WL4 dactylus of female much longer than short, hooked dactyli of WL1–3. Ischium and merus of MXP3 completely fused, without trace of suture; dactylus of palp subspatuliform, subequal in length to propodus, inserted distal to base of propodus ($\frac{1}{3}$ to midway from base). G1 a simple tube, tapering from base to tip, slightly recurved distally.

Etymology.—The genus is named in honor of Otto Bürger, whose key paper in 1895, laid the foundation for much of what has been done recently in pinnotherid taxonomy. The genus name is derived from an arbitrary combination of Bürger's name and *Pinnotheres*. The gender is masculine.

Remarks.—The key diagnostic features of *Buergeres* are the form of the MXP3 (dactylus subspatuliform, inserted well before base of propodus), and relative length of the female WL4 (dactylus much longer than WL1–3). No other group of pinnotherids associated with holothurians has these characters. With regards to the form of the MXP3 and WL4, *Buergeres* is perhaps closest to the American *Tumidotheres* Campos, 1989, but in members of the latter genus, the carapace is less rounded with the front more distinctly produced, and the propodus and dactylus of MXP3 are proportionately shorter (see Campos 1989). *Tumidotheres* is also wholly symbiotic with various bivalves while *Buergeres* is an obligate parasite of holothurians. The relatively subspatuliform dactylus of MXP3 also allies it with Atlantic and eastern Pacific taxa like *Afropinnotheres* Manning, 1993, *Nepinnotheres* Manning, 1993, *Alainotheres* Manning, 1993, and *Raymondia* Campos, 2002 (see Manning 1993a, Campos 2002) but they are quite different in the form of the carapace and legs. Some genera of pinnotherids have adult females with the WL3 longest (e.g., *Arcotheres* Manning, 1993, see Campos & Manning 2001); or WL2 longest (e.g., the Atlantic *Zaops* Rathbun,

1900, and *Waldotheres* Manning, 1993; see Manning 1993a, 1993b; Campos and Manning 2000); but in the case of *Buergeres*, WL1–3 are more or less subequal in length, with the dactylus of WL4 longest and more prominently elongate than the rest. In any case, none of the species in these genera are associated with holothurians.

Of the four species presently referred to *Buergeres*, two, *B. holothuriae* (Semper, 1880) and *B. ortmanni* (Bürger, 1895) are treated here in detail. One of these, *B. decanensis* (Chopra, 1931) was well described and figured by Chopra (1931) and its affinities are not in doubt. *Buergeres tenuipes* (Bürger, 1895) (type locality Ubay, Philippines) was described apparently from only one female specimen, but on the basis of Bürger's (1895:371, pl. 9 fig. 11, pl. 10 fig. 11) figures of the third maxillipeds and walking legs, we have little doubt that it belongs in this genus as well. The type of *B. tenuipes* is apparently lost (see Schmitt et al. 1973:89) and we have not been able to locate it in any of the depositories we have checked.

Buergeres ortmanni (Bürger, 1895)

Fig. 4

Pinnotheres ortmanni Bürger, 1895:384, pl. 9 fig. 30, pl. 10 fig. 28.—Schmitt et al., 1973:61. (See Schmitt et al. (1973:61) for additional references).

Neotype.—Female (11.4 by 9.5 mm) (ZRC 2003.59), in holothurian in coral reef, exposed at edge of reef, Pulau Salu, north-eastern Singapore, coll. R. U. Gooding, 28 April 1967.

Other material examined.—2 females (both 12.5 by 11.8 mm) (ZRC 1965.11.24.14–15), coll. Singapore, no other data.

Diagnosis.—Female carapace almost circular, slightly wider than long, width to length ratio 1.1–1.2; dorsal surface smooth, gently convex; intestinal region slightly depressed. Lateral margins gently convex; sub-branchial surfaces densely setose.

MXP3 with ischium and merus completely fused, without trace of suture, subovate, inner margin subangular at distal $\frac{1}{3}$; exopod relatively stout, outer margin gently convex, with well developed flagellal setae; palp 3-segmented, propodus elongate, longer than dactylus; dactylus spatuliform, articulation point anterior to base of propodus. Chelipeds subequal; inner surfaces of merus, carpus, palm and fingers densely covered with relatively long setae; palm relatively stout; fingers shorter than palm; cutting edges of dactylus and propodus each with sub-basal large tooth and 1 or 2 denticles before it, rest of cutting edges smooth, almost blade-like; tips hooked. WL relatively slender, WL2 > WL1 > WL3 > WL4 in length (basis-ischium to tip of dactylus); dactyli of WL1–3 relatively short, sharply tapering; dactylus of WL4 very long, ca. 3 times as long as those of other legs; dorsal margins of meri of all legs relatively densely lined with setae of various lengths, becoming sparse or absent along distal one-quarter; ventral margins of propodus of all legs relatively densely lined with setae on distal half. Female abdomen with all 6 segments distinct, freely articulating, telson semicircular. Male unknown.

Biology.—This species had been collected from *Holothuria fursocinerea* (see Lanchester 1900). The present specimens were obtained from an unknown host.

Remarks.—Bürger (1895) described *Buergeres ortmanni* (as *Pinnotheres ortmanni*) on the basis of one ovigerous female originally obtained by Semper from "Aibukit" in the Philippines. Bürger's specimen cannot be located in the SMF, USNM or Berlin Museum, and is presumed lost, as Schmitt et al. (1973:61) had indicated. Lanchester (1900) subsequently reported the species from Singapore. No other specimens are known. The present specimens in the ZRC from Singapore agree with the type description and figures well and we are confident they are conspecific. To stabilize the taxonomy of this species (especially since it is the proposed type spe-

cies of *Buergeres*), we hereby select a neotype for *Pinnotheres ortmanni* Bürger, 1895, a female specimen measuring 11.4 by 9.5 mm from Singapore (ZRC 2003.59).

Buergeres holothuriae (Semper, 1880)

Fig. 5

Pinnotheres ortmanni Semper, 1880:105.—Bürger, 1895:381, pl. 9 fig. 27, pl. 10 fig. 26.—Schmitt et al., 1973:49. (See Schmitt et al. (1973:49) for additional references).

Type material.—Lectotype: ovigerous female (10.1 by 9.3 mm) (USNM 032433a), Zamboanga, Philippines, coll. Semper, 1876. Paralectotype: 1 ovigerous female (8.0 by 6.5 mm) (USNM 032433b), same data as lectotype.

Diagnosis.—Female carapace almost circular, slightly wider than long, width length ratio 1.1–1.2; dorsal surface smooth, gently convex. Lateral margins gently convex; sub-branchial surfaces gently setose. MXP3 with ischium and merus completely fused, without trace of suture, subcircular, inner margin rounded; exopod relatively stout, outer margin gently convex, with well developed flagellar setae; palp 3-segmented, propodus elongate, longer than dactylus; dactylus spatuliform, articulation point slightly anterior to base of propodus. Chelipeds subequal; inner surfaces of merus, carpus, palm and fingers covered with relatively long setae; outer surface of chela densely covered with short pubescence; palm relatively stout; fingers shorter than palm, basal one-third covered with dense pubescence; cutting edges of dactylus and propodus each with numerous denticles except for almost unarmed distal $\frac{1}{3}$. WL relatively slender, $WL2 > WL1 > WL3 > WL4$ in length (basis-ischium to tip of dactylus); dactyli of WL1–3 relatively short, distinctly hooked; dactylus of WL4 very long, ca. 5 times as long as those of other legs; dorsal and ventral margins of meri of all legs lined with setae of various lengths; ventral margins of propodus and dactylus

of all legs lined with setae. Female abdomen with all 6 segments distinct, freely articulating, telson semicircular. Male unknown.

Biology.—This species has been collected from *Stichopus variegatus* (see Bürger 1895), although the record from *Holothuria scabra* by Semper may be incorrect (see Schmitt et al. 1973:44).

Remarks.—Semper (1880) described *Buergeres holothuriae* (as *Pinnotheres holothuriae*) from an unspecified number of specimens from Zamboanga on Mindanao island in the Philippines. Bürger (1895) who used Semper's specimens for his study, reported that he had three males and eight females available, all of which are regarded as syntypes. Of these, the USNM has two females. The SMF does not have any specimens. Schmitt et al. (1973:49) had incorrectly stated that the types are no longer extant. The larger female specimen (10.1 by 9.3 mm, USNM 032433a) is here designated as the lectotype of *Pinnotheres holothuriae* Semper, 1880.

Notes on Allied Taxa Symbiotic in Holothurians

The generic affinities of *Ostracotheres holothuriensis* (originally described as *Pinnotheres holothuriensis*) should be re-examined in view of recent systematic developments in the family. The species was described from South Australia and has a two-segmented palp (Baker 1907, Pregonzer 1988), but its carapace form is rather unusual. Two other species, *Pinnotheres pilumnoides* and *Ostracotheres holothuriensis*, have been reported from hosts other than holothurians (see Schmitt et al. 1973). The other species mentioned, all placed in the genus *Pinnotheres* thus far, are obligate parasites of holothurians and are not known from other hosts.

Pinnotheres pilumnoides Nobili, 1905, known only from the Red Sea and Gulf of Aden, is similar to *Holotheres*, with short WL, the last apparently not elongate (al-

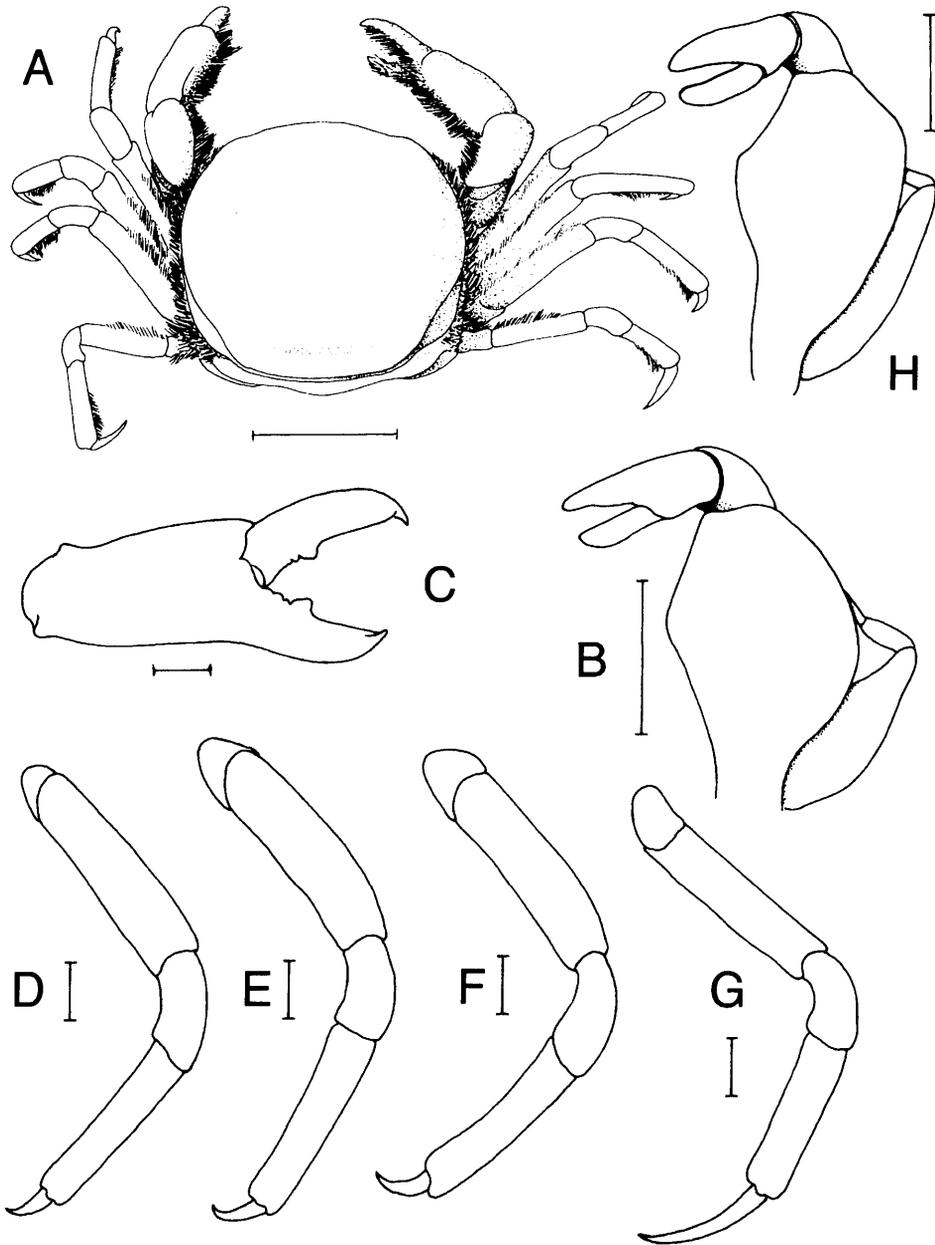


Fig. 4. *Buergeres ortmanni* (Bürger, 1895). A–G, neotype female (11.4 by 9.5 mm) (ZRC); H, female (12.5 by 11.8 mm) (ZRC 1965.11.24.14). A, overall view of specimen; B, H, left MXP3 (denuded), outer view; C, right chela (denuded), outer view; D–G, WL1–4 respectively (denuded). Scales: A = 5.0 mm, B–H = 1.0 mm.

though this is not at all clear from Nobili's (1905, 1906) descriptions, with the dactylus of MXP3 subspatuliform and inserted near the base of the propodus. The dactylus of MXP3 of *P. pilumnoides*, however, is much shorter than the propodus which is also dis-

tinctly shorter compared to other members of the group, and the inner margin of the fused ischio-merus is rounded and not angular (Nobili 1905:308, fig. 12). As such, in some ways, *P. pilumnoides* resembles members of the eastern Pacific *Holothurio-*

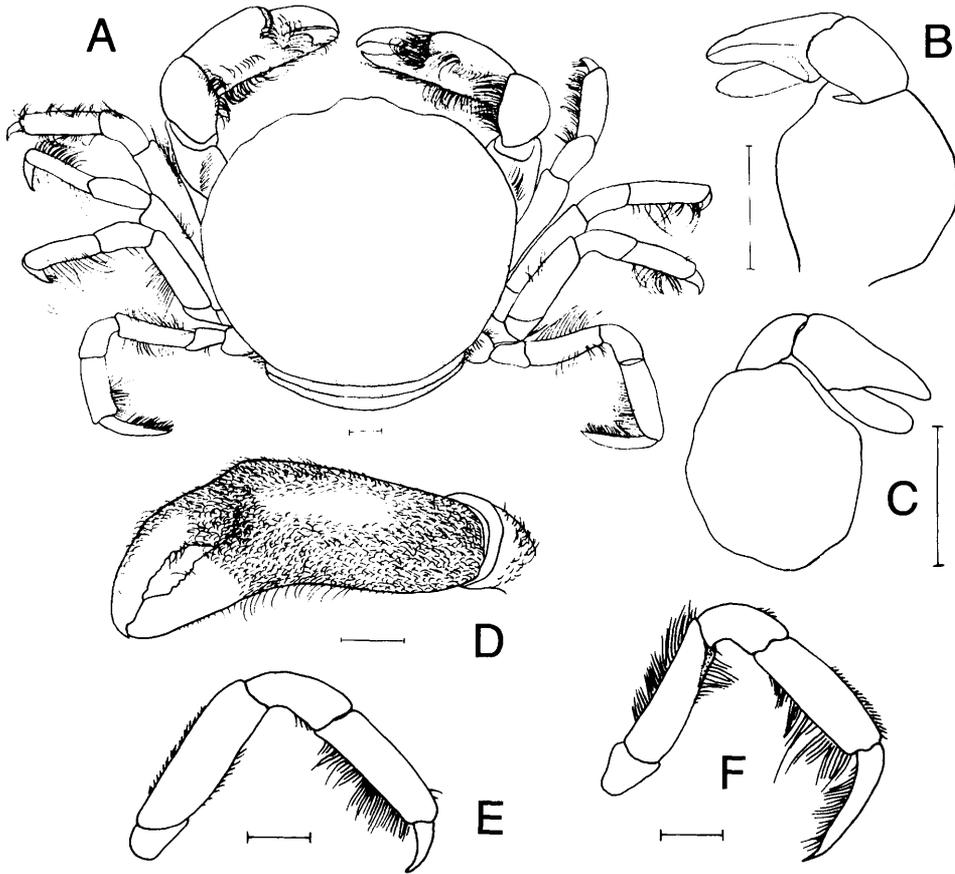


Fig. 5. *Buergeres holothuriae* (Semper, 1880). Lectotype female (10.1 by 9.3 mm) (USNM 032433a). A, overall view of specimen; B, left MXP3 (denuded), outer view; C, left MXP3 (denuded), inner view; C, left chela, outer view; D, WL3 (partially denuded); E, WL4 (partially denuded). Scales = 1.0 mm.

philus (sensu Manning 1993b) although they are clearly not congeneric. We prefer to exclude *P. pilumnoides* from the present discussion until we have an opportunity to examine specimens of the species. Certainly, as things are, *P. pilumnoides* does not fit into any of the Indo-West Pacific pinnotherid genera now recognized.

Alain Manning, 1998, can be distinguished from both *Holotheres* and *Buergeres*, as well as *P. holothuriensis* and *P. pilumnoides*, in the following characters: the spatuliform dactylus of MXP3 is inserted medially rather than proximally on the propodus; the carapace is subcircular, ornamented with few setae dorsally; WL2 and 3 are the longest; the species lives at

slope depths of 399–405 and 457–461 m; the male abdomen comprises only six somites, with the second and third fused; and the apex of male first pleopod is complex rather than simple.

Notes on *Pinnaxodes* and *Holothuriophilus*

The following material has been examined for the following notes. *Pinnaxodes chilensis*: 2 females (14.4 by 12.7 mm, 13.4 by 12.4 mm, carapace broken) (ZMUC), parasite, in rectum of echinoid *Loxechinus albus* (Molina), Chile. *Pinnaxodes major*: 1 female (13.1 by 11.1 mm) (ZMUC), inland sea, from bivalve, coll. K. Hatonaka, 7 May

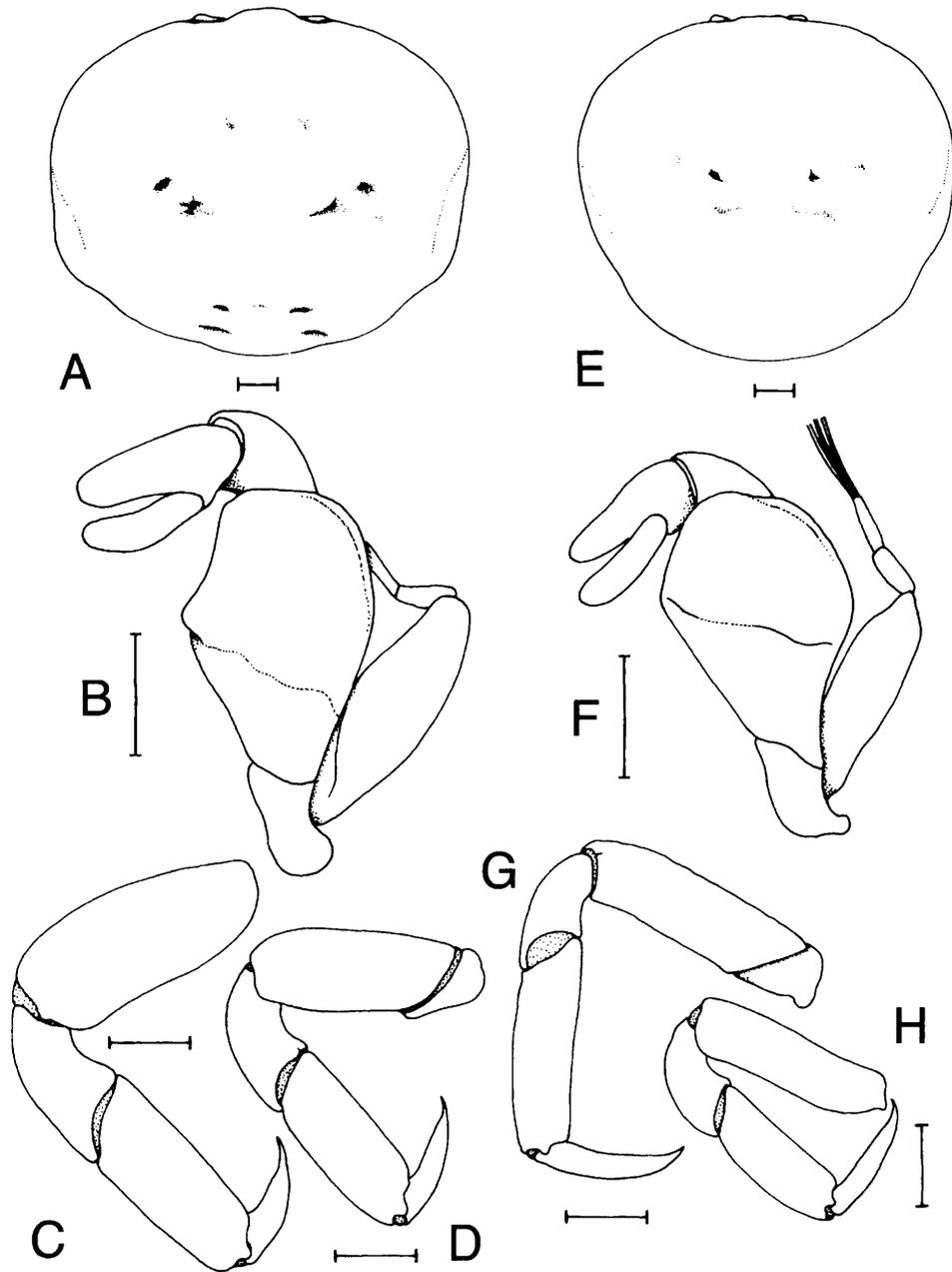


Fig. 6. A–D, *Pinnaxodes major* Ortmann, 1894, female (15.4 by 13.0 mm) (ZRC 1999.39a); E–H, *Pinnaxodes mutuensis* Sakai, 1939, female (14.2 by 12.6 mm) (NSMT). A, E, dorsal views of carapaces; B, F, left MXP3 (outer view); C, G, WL3; D, H, WL4. (All structures denuded.) Scales = 1.0 mm.

1935; 2 females (14.7 by 12.5 mm, 15.4 by 13.0 mm) (ZRC 1999.39), 4 females (NSMT), from *Atrina pectinata*, Hokkaido, Japan, coll. Tsukiji Market, Tokyo, P. K. L. Ng & M. Takeda, 3 February 1999. *Pin-*

naxodes mutuensis: 1 female (14.2 by 12.6 mm) (NSMT), from *Mytilus gallprovincialis*, northern Japan, coll. 19 May 1982.

Some comments on the genus *Pinnaxodes* Heller, 1865 (type species *Pinnaxodes*

hirtipes Heller, 1865, a subjective junior synonym of *Pinnaxodes chilensis* (H. Milne Edwards, 1837)), are necessary as one Indo-West Pacific species, *P. major* Ortmann, 1894, has been reported from a holothurian (Sakai 1939, 1976), although its preferred host seems to be bivalves. Manning (1993b:524, 525) separated *Pinnaxodes* from *Holothuriophilus* on the basis of the carapace shape (greatest width posterior to the midlength, in *Holothuriophilus* it is anterior to the midlength), relatively slender and elongate dactyli of the WL (short and stout in *Holothuriophilus*), and the presence of a suture between the ischium and merus of MXP3 (absent in *Holothuriophilus*). Campos et al. (1998:374) discussed the taxonomy of the American *P. gigas* Green, 1992, and *P. floridensis* Wells & Wells, 1961, including illustrations, and suggested that *Opisthopus* Rathbun, 1893, be regarded as a separate genus (it had been a junior synonym of *Pinnaxodes*).

Takeda & Prince Masahito (2000) discussed the taxonomy of *Pinnaxodes chilensis* (an obligate symbiont of sea urchins), *P. major* and *P. mutuensis* Sakai, 1939 (known only from bivalves), and commented that the latter should be transferred to *Holothuriophilus*. They noted that for *P. mutuensis*, 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." (Takeda & Prince Masahito 2000:110). This, however, is not obvious from their figure (Takeda & Prince Masahito 2000: fig. 2G) that does not show any trace of a suture between the ischium and merus, with only a suture shown between the ischium and basis. We compared specimens of all three species, and the MXP3 of *P. major* (Fig. 6B) is essentially similar to that of *P. mutuensis* (Fig. 6F), with a distinct suture present between the ischium and basis, but the ischium and merus are completely fused, with only the faint trace of a suture demar-

cating the two segments, most clearly seen under transmitted light. This is the same as in *P. chilensis*, although the suture between the ischium and merus in the present specimen cannot be easily seen (Fig. 7A), being very faint. However, the MXP3 of *P. major* and *P. mutuensis* differ from that of *P. chilensis* in that the latter has the dactylus and propodus proportionately shorter (Fig. 7A, B). Campos et al. (1998) had commented that *P. gigas* and *P. floridensis* have the male telsons "basally expanded", forming a more rounded or pentagonal structure (Campos et al. 1998: fig. 3A, C). This is also the case for *P. major* (see Takeda & Prince Masahito 2000: fig. 4B), but not *P. mutuensis* (see Takeda & Prince Masahito 2000: Fig. 5L). In addition, while *P. gigas*, *P. floridensis* and *P. major* have their fronts distinctly produced anteriorly (Fig. 6A; Campos et al. 1998: fig. 2A, C; Takeda & Prince Masahito 2000: fig. 4A), the front barely extends beyond the orbits in *P. mutuensis* (Fig. 6E; Takeda & Prince Masahito 2000: Fig. 5A, I, J). These differences suggest that *P. mutuensis* is not a true *Pinnaxodes*. However, to refer *P. mutuensis* to *Holothuriophilus* as suggested by Takeda & Prince Masahito (2000) is also unsatisfactory. Species of *Holothuriophilus* have quadrate carapaces which are clearly wider than long (rather than round) and the WL are proportionally shorter (Fig. 7D-F; Manning 1993b: figs. 2a, 3). It is also pertinent to note that while members of *Holothuriophilus* are symbiotic in holothurians, *P. mutuensis* is only known from bivalves. For the moment, we retain *Pinnotheres mutuensis* in *Pinnaxodes* for lack of a better classification. It may need to be referred to its own genus at a later date.

The MXP3 of *P. chilensis* (Fig. 7A, B) actually closely resembles that of *Holothuriophilus* (see Manning 1993b: fig. 2b, c; present Fig. 7C), and interestingly, both taxa are from the eastern Pacific. With regards to the other supposed differences between *Pinnaxodes* and *Holothuriophilus* mentioned by Manning (1993b), we find

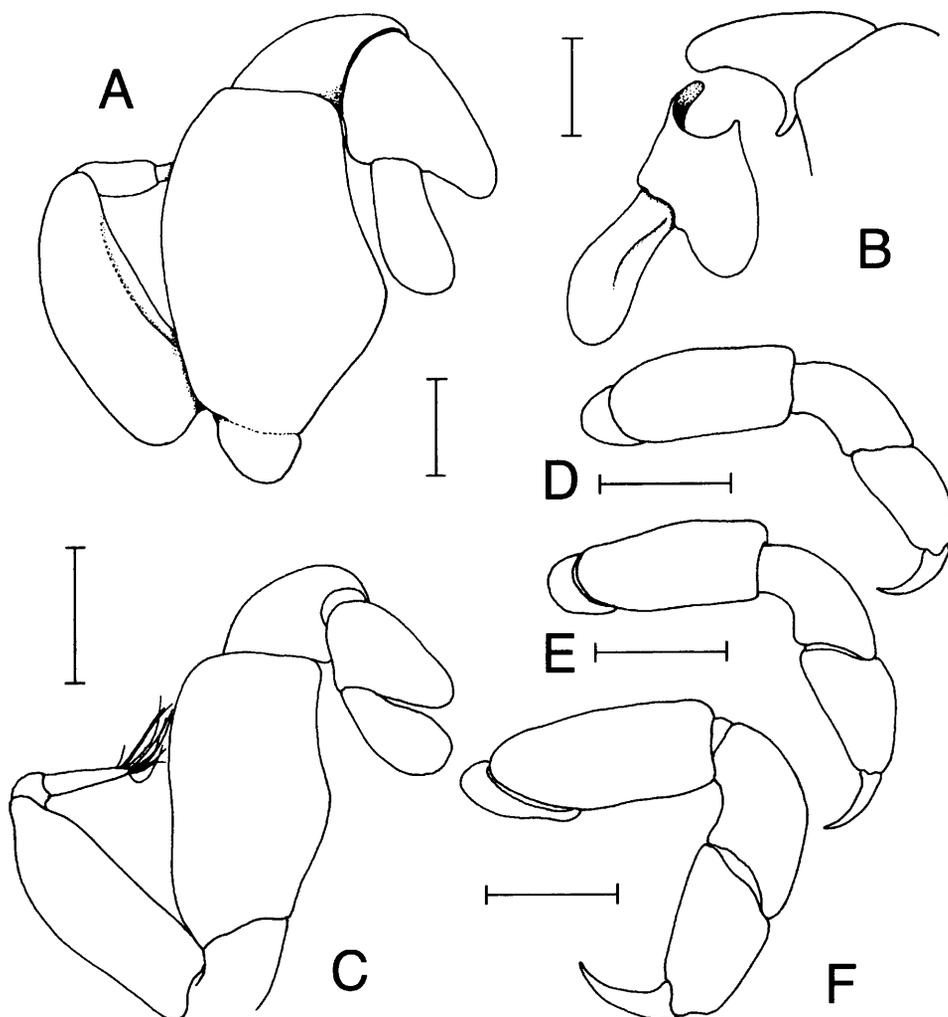


Fig. 7. A, B, *Pinnaxodes chilensis* (H. Milne Edwards, 1837), female (14.4 by 12.7 mm) (ZMUC), A, outer surface of right MXP3, setae removed, suture between ischium and merus very faint, not drawn; B, inner surface of right MXP3, setae removed, propodus and dactylus detached. C–F, *Holothuriophilus trapeziformis* Nauck, 1880, lectotype female (7.7 by 4.8 mm) (SMF); C, right MXP3; D–F, WL2–4 respectively. (All structures denuded.) Scales = 1.0 mm.

the difference in carapace shape not at all obvious, especially between *P. major* and *H. trapeziformis*. The proportions of the dactyli of the WL are also not that distinct, with those of *Holothuriophilus* only slightly shorter than those of the three *Pinnaxodes* species examined here (Fig. 7D–F).

With regard to the specimen of *Holothuriophilus trapeziformis* in the SMF, it carries the old catalogue number “ZMG 67/565a” and was collected from Mazatlán,

Sinaloa, in México. Nauck (1880:24, 66) did not state how many specimens he had or even where it was from, commenting only that it was a “Parasit in *Holothuria maxima* Semper” (Nauck 1880:66). Bürger (1895:380) subsequently listed one female (as *Pinnotheres trapeziformis*) measuring 8.5 by 5.0 mm from Mazatlán, from *Holothuria maxima* Semper. De Man (1887:722) also measured one specimen from Nauck, noting it was a female 13.8 by 10.5

mm. The size discrepancy between Bürger's and De Man's specimens is difficult to reconcile and suggests that Nauck may have had more than one specimen. As such, we prefer to regard the present SMF specimen as a syntype and we here designate it as the lectotype of *Holothuriophilus trapeziiformis* Nauck, 1880. The present female specimen in the SMF (Fig. 7C–F) measures approximately 7.7 by 4.8 mm, closer to Bürger's data. This specimen is in poor condition, with the carapace removed, very soft and somewhat deformed (making precise measurements difficult).

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Literature Cited

- Baker, W. H. 1907. Notes on South Australian Decapoda Crustacea. Part V.—Transactions, Proceedings and Report of the Royal Society of South Australia 31:173–191, pls. 23–25.
- Bosc, L. A. G. 1802. Histoire naturelle des Crustacés, contenant leur description et leurs moeurs, avec figures dessinées d'après nature. Deterville, Paris, 1:1–258, pls. 1–8; 2:1–296, pls. 9–18.
- Bürger, O. 1895. Ein Beitrag zur Kenntniss der Pinnotherinen.—Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere 8:361–390, pls. 9. 10.
- Campos, E. 1989. *Tumidotheres*, a new genus for *Pinnotheres margarita* Smith, 1869, and *Pinnotheres maculatus* Say, 1818 (Brachyura: Pinnotheridae).—Journal of Crustacean Biology 9:672–679.
- . 2002. Two new genera of pinnotherid crabs from the tropical eastern Pacific (Decapoda: Brachyura: Pinnotheridae).—Journal of Crustacean Biology 22:328–336.
- , & R. B. Manning. 2000. The identities of *Pinnotheres nudus* Holmes, 1895, and *P. nudus* sensu Weymouth, 1910 (Crustacea: Decapoda: Pinnotheridae).—Proceedings of the Biological Society of Washington 113:799–805.
- , & ———. 2000. Authorship and diagnosis of the genus *Arcotheres* Manning, 1993 (Crustacea: Brachyura: Pinnotheridae).—Raffles Bulletin of Zoology 49:167–170.
- , V. Díaz, & J. A. Gamboa-Contreras. 1998. Notes on distribution and taxonomy of five poorly known species of pinnotherid crabs from the eastern Pacific (Crustacea: Brachyura: Pinnotheridae).—Proceedings of the Biological Society of Washington 111:372–381.
- Chopra, B. 1931. Further notes on Crustacea Decapoda in the Indian Museum. II. On some decapod crustacea found in the cloaca of holothurians.—Records of the Indian Museum 33(3):303–324.
- Chuang, S. H. 1961. On Malayan Shores. Muwu Shosa, Singapore, 225 pp.
- Doflein, F. 1904. Brachyura. Wissenschaften Ergebnisse Deutschen Teifsee 'Valdivia' Expedition 6: i–xiv, 1–314, figs. 1–68, pls. 1–57.
- Garth, J. S. 1957. The Crustacea Decapoda of Chile. Reports of the Lund University Chile Expedition 1948–49, 29.—Lunds Universitets Arsskrift, new series (2)53(7):1–130.
- Green, T. M. 1992. *Pinmaxodes gigas*, a new species of pinnotherid crab from the Gulf of California (Decapoda: Brachyura: Pinnotheridae).—Proceedings of the Biological Society of Washington 105:775–779.
- Hamel, J.-F., P. K. L. Ng, & A. Mercier. 1999. Life cycle of the pea crab *Pinnotheres halangi* sp. nov., an obligate symbiont of the sea cucumber *Holothuria scabra* Jaeger.—Ophelia 50(3):149–175.
- Heller, C. 1865. Crustaceen. In Reise der österreichischen Fregatte 'Novara' um die Erde, in den Jahren 1857, 1858, 1859, unter den Befehlen des Commodore B. von Wüllerstorff-Urbair. Zoologische Theil 2(3):1–280, pls. 1–25.
- Lanchester, W. F. 1900. On a collection of crustacea made at Singapore and Malacca.—Part I. Crustacea Brachyura.—Proceedings of the Zoological Society of London 1900:719–770, pls. 44–47.
- Man, J. G. De. 1887. Uebersicht 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 für Systematik, Geographie und Biologie der Thiere 2: 639–689, pl. 1.
- Manning, R. B. 1993a. West African pinnotherid crabs subfamily Pinnotherinae (Crustacea, Decapoda, Brachyura).—Bulletin du Muséum national d'Histoire naturelle, Paris (4)15A(1–4):125–177.
- . 1993b. Three genera removed from the synonymy of *Pinnotheres* Bosc, 1802 (Brachyura: Pinnotheridae).—Proceedings of the Biological Society of Washington 106:523–531.
- . 1998. A new genus and species of pinnotherid crab (Crustacea, Decapoda, Brachyura) from Indonesia.—Zoosystema, Paris 20(2):357–362.
- Milne Edwards, H. 1837. Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux. Atlas [1834, 1837, 1840]: 1–32, plates 1–14, 14 bis, 15–25, 25 bis, 26–42. Librairie Encyclopédique de Roret, Paris.
- Nauck, E. 1880. Das Kaugerüst der Brachyuren (mit beschreibung neuer gattungen und arten, Z. T. von C. Semper).—Zeitschrift wissenschaften Zoologische Leipzig 34:1–69, pl. 1.
- Nobili, G. 1901. Decapodi raccolti dal Dr. Filippo Silvestri nell'America meridionale.—Bolletino dei Museo di Zoologia ed Anatomia comparata della R. Università di Torino 16(402):1–16.
- . 1905. Décapodes nouveaux des côtes d'Arabie et du Golfe Persique. (Diagnoses préliminaires).—Bulletin du Muséum national d'Histoire naturelle, Paris 11(3):158–164.
- . 1906. Faune carcinologique de la Mer Rouge. Décapodes et stomatopodes.—Annales de Sciences Naturelles Zoologie, Paris (9)4(1–3):1–347, pls. 1–11.
- Ortmann, A. 1894. 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. VIII. Theil. Abtheilung: Brachyura (Brachyura genuine Boas) III. Unterabtheilung: Cancroidea, 2. section: Cancrinae, 2. Gruppe: Catametopa.—Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere 7:683–772, pl. 23.
- Poeppig, E. 1836. Crustacea chilensia nova aut minus nota descripsit.—Archiv für Naturgeschichte 2(1):134–144, pl. 4.
- Pregenz, C. 1988. A redescription of *Pinnotheres holothuriensis* Baker, 1907 and *Pinnotheres subglobosus* Baker, 1907 with a reassignment to the genus *Ostracotheres* (Decapoda, Brachyura).—Crustaceana 55:17–28.
- Rathbun, M. J. 1893. Scientific results of explorations by the U.S. Commission Steamer 'Albatross'. XXIV. Description of new genera and species of crabs from the west coast of North America and the Sandwich Islands.—Proceedings of the United States National Museum 16:223–260.
- . 1900. The catametopous or grapsoid crabs of North America.—American Naturalist 34:583–592.
- . 1918. The grapsoid crabs of America.—Bulletin of the United States National Museum 97: 1–461.
- Sakai, T. 1939. Studies on the crabs of Japan. IV. Brachygnatha, Brachyrhyncha. Tokyo, pp. 365–741, pls. 42–111.
- . 1976. Crabs of Japan and the adjacent seas. In three volumes; English text, pp. xxix+773pp., Japanese text, pp. 1–461, Plates volume, pp. 1–16, pls. 1–251. Kodansha Ltd., Tokyo.
- Schmitt, W. L., J. C. McCain, & E. Davidson. 1973. Decapoda I. Brachyura I. Fam. Pinnotheridae. Crustaceorum Catalogus, Dr. W. Junk, Den Haag 3:1–160.
- Semper, K. 1880. Natürlichen existenzbedingungen der Thiere. Erster theil. F. A. Brockhaus, Leipzig. Pp. 98–100.
- Takeda, M., & Prince Masahito. 2000. Systematic notes on the pinnotherid crabs of the genus *Pinnaxodes* (Crustacea: Decapoda: Brachyura).—Bulletin of the National Science Museum, Series A (Zoology) 20:99–112.
- Tesch, J. J. 1918. Decapoda Brachyura II. Goneplacidae and Pinnotheridae.—Siboga Expeditie Monographite 39c1:149–295, pls. 7–18.
- Van den Spiegel, D., & M. Jangoux. 1989. Sur la symbiose entre le Pinnotheride *Pinnotheres villosissimus* (Crustacea, Decapoda) et l'Holothurie *Actinopyga mauritiana* (Echinodermata).—Vie Marine, Marseille 10:205–213.
- Wells, H. W., & M. J. Wells. 1961. Observations on *Pinnaxodes floridensis*, a new species of pinnotherid crustacean in holothurians.—Bulletin of Marine Science of the Gulf and Caribbean 11:267–279.