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REVISION OF THE GENUS *ECHINOECUS* (DECAPODA: BRACHYURA: EUMEDONIDAE), CRABS SYMBIOTIC WITH SEA URCHINS

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ABSTRACT

The taxonomy of *Echinoecus*, a genus of crabs symbiotic with sea urchins, is revised. The genus *Proechinoecus* is a synonym of *Echinoecus*. *Echinoecus*, as here defined, contains 3 species: *E. pentagonus*, *E. nipponicus*, and *E. sculptus*.

The best known genus among eumedonid crabs is *Echinoecus* Rathbun, 1894. The genus is generally regarded as monotypic with only one widely distributed species, *E. pentagonus* (A. Milne Edwards, 1879). There are, however, a host of synonyms (Števčić *et al.*, 1988). *Echinoecus pentagonus*, a symbiont of sea urchins (Echinodermata: Echinoidea), has been well studied ecologically (e.g., Castro, 1971, 1978). Ward (1934) described a new genus and new species of an echinoid-dwelling crab, *Proechinoecus sculptus*, from Christmas Island, but very little is known about it.

The present paper reexamines most of the type material of *Echinoecus pentagonus* and its synonyms, as well as *Proechinoecus sculptus*. As a result, *Proechinoecus* Ward, 1934, is synonymized under *Echinoecus* Rathbun, 1894, and three species of *Echinoecus* are now recognized: *E. pentagonus* (A. Milne Edwards, 1879), *E. nipponicus* Miyake, 1939, and *E. sculptus* (Ward, 1934).

MATERIALS AND METHODS

The abbreviations G1 and G2 are used for the first and second male pleopods, respectively. Measurements are those of the carapace length and width, respectively. The length of the carapace was measured from the tip of the rostrum to the posterior margin of the carapace; the width was taken from one anteroposterior angle to the other.

Specimens examined are deposited in: BMNH—Natural History Museum (former British Museum (Natural History)), London, United Kingdom; BNHM—Beijing Natural History Museum, Beijing, China; BPBM—Bishop Museum, Honolulu, Hawaii, U.S.A.; IZAS—Institute of Zoology, Academia Sinica, Beijing, China; KMNH—Kitakyushu Museum of Natural History, Kitakyushu, Japan; MNHN—Muséum national d'Histoire naturelle, Paris, France; NSMT—National Science Museum, Tokyo, Japan; RMNH—Nationaal Natuurhistorisches Museum (former Rijksmuseum van Natuurlijke Histoire), Leiden, The Netherlands; SMF—Forschungsinstitut Senckenberg, Frankfurt am Main, Germany; USNM—National Museum of Natural History, Smith-

sonian Institution, Washington, D.C., U.S.A.; WAM—Western Australian Museum, Perth, Australia; and ZRC—Zoological Reference Collection of the Raffles Museum, Department of Biological Sciences, National University of Singapore.

SYSTEMATICS

Genus *Echinoecus* Rathbun, 1894

- Eumedon* A. Milne Edwards, 1879: 104 [incorrect spelling of *Eumedon* H. Milne Edwards, 1834].
- Echinoecus* Rathbun, 1894: 43, 66; Ward, 1934: 7; Miyake, 1939: 83, 86; Serène *et al.*, 1958: 137, 138 [in key], 142, 234; Serène and Romimohtarto, 1963: 2; Sakai, 1976: 294 [volume in English], 177 [volume in Japanese]; Wu, 1983: 121 [name in Chinese]; Van Dover *et al.*, 1986: 757 [larvae]; Števčić *et al.*, 1988: 1309, 1317.
- Liomedon* Klunzinger, 1906: 56, 89 [type species *Liomedon pentagonus* Klunzinger, 1906, by monotypy]; Serène *et al.*, 1958: 142, 145, 234, 240.
- Eumedonus* — Laurie, 1915: 408, 411 (part); Balss, 1922: 137 (part); Flipse, 1930: 18, 20 [in key] (part); Monod, 1938: 111 (part); Sakai, 1938: 347 (part); Buitendijk, 1950: 72 (part); Barnard, 1954: 95; Barnard, 1955: 18 (part); Serène *et al.*, 1958: 142, 145, 148, 235 [not *Eumedonus* H. Milne Edwards, 1834].
- Proechinoecus* Ward, 1934: 5, 7; Miyake, 1939: 87; Balss, 1957: 1631; Serène *et al.*, 1958: 138 [in key], 240; Števčić *et al.*, 1988: 1312, 1317.

Type Species.—*Echinoecus pentagonus* Rathbun, 1894 (= *Eumedon pentagonus* A. Milne Edwards, 1879), by monotypy. Gender of genus masculine.

Etymology.—The name was probably derived from the name of the sea urchin (Echinoidea) and Greek *oikos* meaning home, alluding to the symbiotic habits of the type species. Gender masculine.

Diagnosis.—Carapace oval, rostrum short to very elongate; inner supraorbital teeth absent; regions poorly defined; surfaces of carapace, chelipeds, and ambulatory legs smooth to punctate, without granules; dorsal surface of carapace glabrous, never covered with pubescence. Antero- and posterolateral margins

clearly demarcated, sometimes by small tooth or angle; anterolateral margin entire, without teeth, lobes, or crest, margin rounded. Antennules folding obliquely, 60–70° from horizontal, appearing almost vertical. Eyes small, well developed, sometimes hidden by carapace in larger specimens. Second antennal segment short, length of second antennal segment subequal to width. Chelipeds smooth to punctate; carpus with one sharp inner distal spine, merus with single inner and single outer distal tooth; chela short, stout; fingers not carinate, pollex not bent downward. Ambulatory leg segments smooth, subcylindrical; merus subcristate; dactylus of first leg not longer than those of other legs.

Remarks.—Alphonse Milne Edwards (1879) described *Eumedon pentagonus* from Mauritius. The use of the spelling of the generic name *Eumedon*, however, cannot be construed as the recognition of *Eumedon* as a new genus. It is obvious that A. Milne Edwards (1879) incorrectly used the spelling *Eumedon* in place of *Eumedonus*. Whenever he established a new genus (e.g., *Goniothorax* and *Rhabdonotus*), he introduced it as such (i.e., by adding the suffix nov. gen.), gave the author's name, and provided a diagnosis of each. For *Eumedon pentagonus*, however, A. Milne Edwards introduced the species as new (as a nov. sp.), but without comments on the genus. In his descriptions, Henri Milne Edwards (1834: 348) always provided a vernacular name before the scientific name for each genus and species, and for *Eumedonus*, he introduced the genus as "Genre EUMEDON—*Eumedonus*" (H. Milne Edwards, 1834: 349). In describing the type (and only) species, he introduced it as "EUMÉDON NEGRE.—*E. niger*" (H. Milne Edwards, 1834: 350). In his synoptic table, he used the vernacular name "EUMÉDON" for the genus (H. Milne Edwards, 1834: 348). The use of the spelling "Eumedon" by A. Milne Edwards (1879) should thus be regarded as an incorrect spelling of *Eumedonus*.

Rathbun (1894) was the first to establish the correct generic name, *Echinoecus*, for this group of crabs, although most workers (e.g., Laurie, 1915; Balss, 1922) tended to follow A. Milne Edwards (1879) in using the name *Eumedonus* when referring to the present genus. Ward (1934) was the first to follow Rathbun, and subsequently, Miyake (1939) and Serène *et al.* (1958) also agreed that

Echinoecus should be regarded as different from *Eumedonus* sensu stricto. *Echinoecus* clearly differs from *Eumedonus* in the form of the carapace, the folding angle of the antennule, and structures of the eye and G1. In *Echinoecus*, the anterolateral margin is rounded or marked by a small tooth. The antennule is very oblique (appearing almost vertical), the eyes are smaller and may be hidden by the carapace, and the G1 is stouter and shorter. In *Eumedonus*, however, the anterolateral margin always has a distinct tooth, the antennule is only slightly oblique (approximately 45°), the eyes are larger, and the G1 is longer and more slender.

Echinoecus, as now recognized, has three species, one (*E. pentagonus*) that ranges from east Africa to the Hawaiian Islands, the widest distribution of any known eumedonid. The characters of the genus are distinctive, especially with regard to the carapace form and obliquely folding (almost vertical) antennules. The similarity of *Echinoecus* to *Proechnoecus* Ward, 1934, is very apparent. Serène and Romimohtarto (1963: 3) suggested the "... possible inclusion of the two genera *Proechnoecus* and *Echinoecus* in one . . .", although they noted differences between them. In *Proechnoecus*, the anterolateral angle almost always bears a small tooth (completely rounded in *Echinoecus pentagonus*, the type species of *Echinoecus*), the carapace and sternum are proportionately broader, with the carapace rectangular, the rostrum is shorter, the G1 is slightly shorter and stouter (slightly longer and more slender in *Echinoecus*), and there is a marked sexual dimorphism. Nonetheless, we feel that in comparison with other genera of the Eumedonidae, these characters are not valid at the generic level. Accordingly, *Proechnoecus* Ward, 1934, is here regarded as a junior subjective synonym of *Echinoecus* Rathbun, 1894.

The genus *Echinoecus* now contains three species, *E. nipponicus* Miyake, 1939, *E. pentagonus* (A. Milne Edwards, 1879), and *E. sculptus* (Ward, 1934). All these species are obligate symbionts of sea urchins.

KEY TO SPECIES OF *ECHINOECUS*

1. Sharp lateral carapace tooth present in adults; rostrum short, broad; anterior margin of ambulatory merus extending in small distal tooth; anterior thoracic sternite segments broad, surface smooth to heavily pitted; G1 stout, short 2

- Lateral carapace tooth absent in adults; rostrum long, sharp; anterior margin of ambulatory merus rounded distally; sternite segments narrow; thoracic sternum heavily pitted; G1 long, slender
..... *E. pentagonus* (A. Milne Edwards, 1879)
- 2. Frontal margin trilobed; anterior thoracic sternites mildly pitted; sexual dimorphism present (carapace of female heavily pitted with fossae)
..... *E. sculptus* (Ward, 1934), new combination
- Frontal margin triangular; anterior thoracic sternites smooth; sexual dimorphism absent (carapace of females not pitted with fossae)
..... *E. nipponicus* Miyake, 1939

Echinoecus pentagonus
(A. Milne Edwards, 1879)
Figs. 1, 2A–P, 4H

- Eumedon pentagonus* A. Milne Edwards, 1879: 104 [type locality Mauritius, Indian Ocean]; Serène *et al.*, 1958: 148, 235 [list only].
- Echinoecus pentagonus* Rathbun, 1894: 43, 66 [type locality Port Lloyd, Bonin (= Ogasawara) Islands, Japan]; Rathbun, 1906: 832, 880, fig. 37 [Oahu, Hawaiian Islands]. Miyake, 1939: 84, 88 [in key] [list only]; Serène, *et al.*, 1958: 148, 151 [in key], 152, 235, figs 11, 2, 3, pl. 4: fig. A [Nhatrang, Vietnam]; Guinot, 1966: 299 [as "*E. pentagonus* (Rathbun)"]; list only]; Serène, 1968: 63 [list only]; Castro, 1971: 229, figs. 1, 2, 5, 6 [Hawaiian Islands]; Anonymous, 1974: 125 [South China Sea]; Serène *et al.*, 1974: 20 [Ambon, Moluccas = Maluku Islands, Indonesia]; Chen, 1975: 158, 179, fig. 1 [Xisha Islands = Parcel Islands, South China Sea]; Sastry, 1977: 120 [Nicobar Islands, Andaman Sea]; Castro, 1978: 259 [Hawaiian Islands] [larvae]; Sastry, 1981: 20, 26 [Nicobar Islands, Andaman Sea]; Wu, 1983: 121 [name in Chinese]; Mather and Bennett, 1984: 66, fig. 36.119 [Heron Island, Queensland, Australia]; Dai *et al.*, 1986: 162, fig. 94 [Xisha Islands = Parcel Islands, South China Sea]; Van Dover *et al.*, 1986: 757, figs. 1–5 [Hawaiian Islands] [larvae]; Nagai and Nomura, 1988: 221 [color photograph] [Okinawa, Ryukyu Islands, Japan]; Števcič *et al.*, 1988: 1309 [Phuket Island, Andaman Sea; Solomon Islands; Line Islands, Pacific Ocean]; Soltanpur-Gargari *et al.*, 1989: 70 [larvae]; Dai and Yang, 1991: 180, fig. 94 [Xisha Islands = Parcel Islands, South China Sea]; Mori *et al.*, 1991: 302 [list only].
- Eumedon convictor* Bouvier and Seurat, 1905: 629 [type locality Hao, Tuamotu Islands, French Polynesia; additional record from New Guinea]; Nobili, 1907: 382 [types reexamined]; Klunzinger, 1913: 102 [Red Sea]; Balss, 1922: 137 [note only]; Mortensen, 1940: 171, 294 [Mauritius]; Serène *et al.*, 1958: 155, 166, 235 [note only].
- Liomedon pentagonus* Klunzinger, 1906: 57, 89, pl. 2: figs. 11, 11a–d [type locality Red Sea]; Balss, 1922: 137 [note only]; Serène *et al.*, 1958: 145, 148, 152, 236 [note only].
- Eumedon convictor*—Laurie, 1915: 408, 411 [list only]; Clark 1950: 56 [Cocos (Keeling) Islands, Indian Ocean]; Tweedie, 1950: 107 [Cocos (Keeling) Islands, Indian Ocean]; Holthuis, 1953: 6 [Raroia Atoll, Tuamotu Islands, French Polynesia]; Morrison, 1954: 6 [as "*Eumedon convictor*"; Raroia Atoll, Tuamotu Islands, French Polynesia]; Serène *et al.*, 1958: 145, 152, 166, 236 [note only]; Yang 1979: 11 [Cocos (Keeling) Islands, Indian Ocean].
- Eumedon petiti* Gravier 1922: 484 [type locality Tulear, Madagascar]; Flipse, 1930: 80, 90 [list only]; Miyake, 1939: 85, 88 [in key] [note only]; Serène *et al.*, 1958: 145, 148, 149, 151, 152, 155, 157, 236 [note only].
- Eumedon pentagonus*—Balss, 1922: 137 [Bonin (= Ogasawara) Islands, Japan]; Balss, 1924: 70 [list only]; Flipse, 1930, 80, 90 [list only]; Monod, 1938: 111, 112 [list only]; Serène *et al.*, 1958: 236 [list only]; Michel, 1964: 7 [list only].
- Echinoecus rathbunae* Miyake, 1939: 84, 88 [in key], 92, figs. 1A, 2A, 3A [type locality Hutami Harbor, Bonin (= Ogasawara) Islands, Japan]; Serène *et al.*, 1958: 149, 151, 152, 155, 156, 157, 235 [note only].
- Echinoecus rathbunae convictor* Miyake, 1939: 84, 88 [in key] [list only]; Serène *et al.*, 1958: 149, 151, 152, 157, 235 [note only].
- Echinoecus klunzingeri* Miyake, 1939: 85, 88 [in key] [list only] [as replacement name for *Liomedon pentagonus* Klunzinger, 1906]; Serène *et al.*, 1958: 149, 151, 152, 235 [note only].
- Material Examined**—Holotype: ♂ (8.5 × 7.9 mm) (MNHN-B 24731) Mauritius, collected by A. Milne Edwards. Others: Red Sea: 1 ♂ (RMNH 42943), Gulf of Aqaba, Elat, Israel, on *Echinothrix* sp., collected by H. Schumacher, February 1976; 4 ♂♂, 4 ♀♀ (BMNH 1974.571), Port Sudan, from sea urchin, collected by N. Polumin. Kenya: 2 ♂♂ (USNM 143806, 143807), Ras Inatine, Mombassa, coral reef, on *Diadema setosum* (Leske), collected by A. J. Bruce; 2 ♂♂ (BMNH 1985.335), between Mombassa beach and Nyale Barnacles, low tide, on sea urchin *Diadema savignyi* (Michelin), collected by M. Good, 24 March 1985; 2 ♀♀ (BMNH 1974.572), Kikambala, outer edge of reef, from sea urchin, collected by N. Polumin, 23 July 1971; 2 ♀♀ (BMNH 1985.336), off Nyale Beach, associated with sea urchin *Diadema setosum*, collected by M. Good, 26 April 1985; 1 ♂ (USNM 143807), littoral coral reef, Ras Liwatoni Bay, Mombassa, collected by A. J. Bruce, 8 February 1973; 1 ♂ (USNM 143806), littoral coral reef, Ras Liwatoni Bay, Mombassa, collected by A. J. Bruce, 8 February 1973. Madagascar: 1 ♂ (8.7 × 7.3 mm), 1 ♀ (5.7 × 6.9 mm) (syntypes of *Eumedon petiti*, MNHN-B 24732), Tulear, collected by Petit. Seychelles: 1 ♂ (11.7 × 9.7 mm), 1 ♀ (RMNH D42518), Mahé, southwest coast, Baie Lazare/Anse Gaulettes, SEY 602 NIOP-E, station 602, 04°46'S, 55°29'E, 2–4 m, sandy bay with calcareous barrier, snorkeling, on sea urchin. Cocos-Keeling Islands: 4 ♀♀ (ZRC 1965.10.19.78–82), collected by M. Tweedie, 1941. Thailand: 1 ♀ (PMBC 2469), Ko Mai Thon, Phuket, on *Echinothrix calamaris*, 13 May 1980. Indonesia: 1 ♀ (NSMT Cr 11322), Pombo Island, Ambon, Moluccas (= Maluku) collected 28 November 1992. Philippines: 1 ♂, 1 ♀ (MNHN-B 25683), Mactan, Cebu Province, 10°17'N, 124°00'E, on *Echinothrix calamaris*, collected by P. Bouchet, 10 June 1985. China: 1 ♀ (ovigerous) (IZAS), Xisha (= Parcel) Islands, South China Sea, collected 26 April 1957; 1 ♀ (BNHM), Jing-Ying Island, Xisha (= Parcel) Islands, South China Sea, collected 11 March 1976. Japan: 1 ♀ (USNM 13889) (holotype of *Echinoecus pentagonus* Rathbun, 1894), from intestinal canal of *Echinothrix calamaris*, Port Lloyd, Bonin Islands; 1 ♂ (ZRC 1997.153), Zamami Island, Okinawa, on *Echinothrix diadema*, collected by S. Nagai, 1980; 1 ♀ (NSMT), Kushimoto, Wakayama Prefecture, on *Pseudocentrotus depressus*, collected 4 November 1973; 1 ♂ (NSMT 841221), Sesoko-jima, Okinawa, on *Heterocentrotus mammillatus*, no other data. Australia: 1 ♂ (WAM 1280–85), southwest corner, Clarke

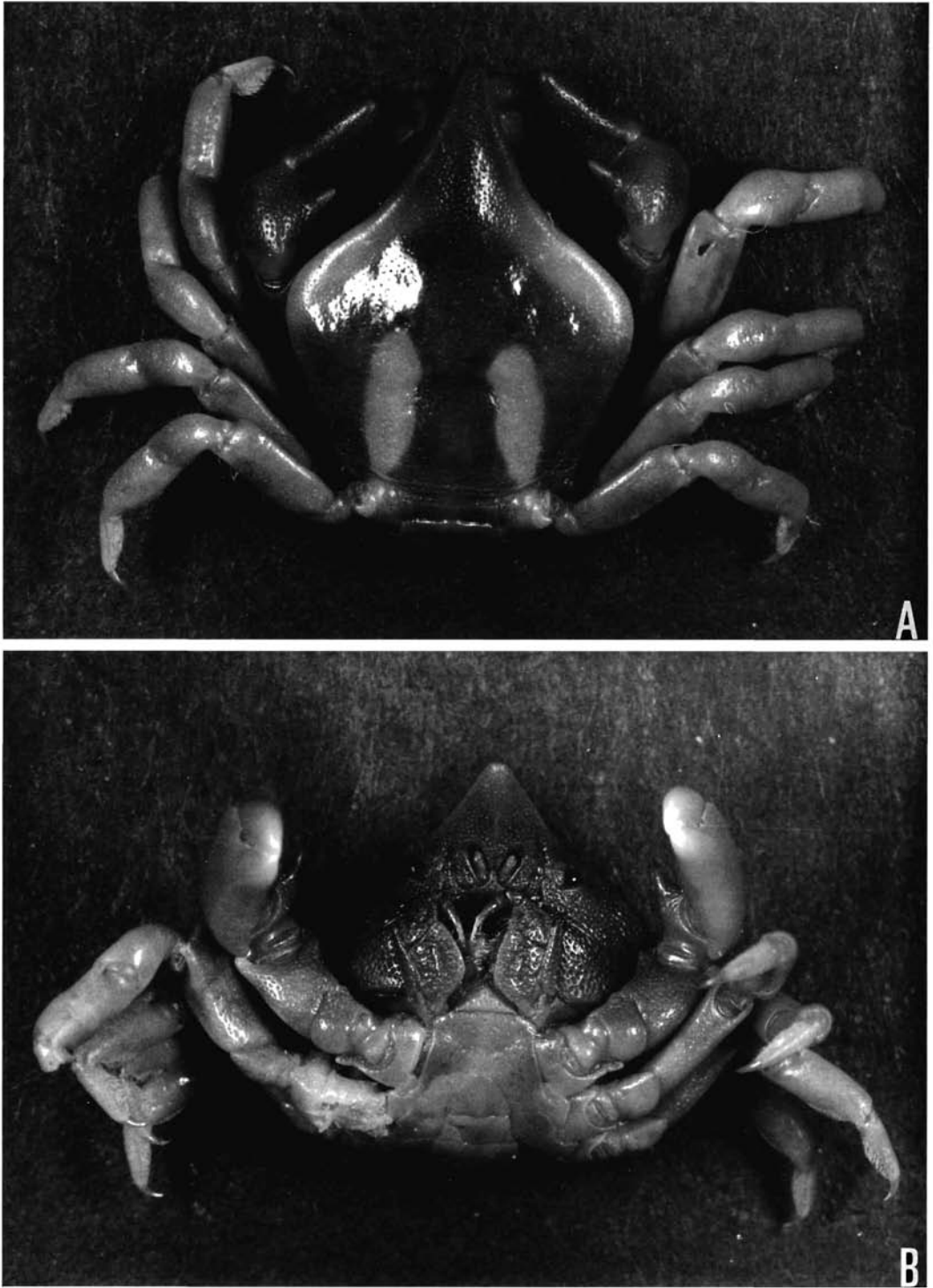


Fig. 1. *Echinoecus pentagonus* (A. Milne Edwards, 1879), male, 11.7 × 9.7 mm, Mahe, Seychelles (RMNH 42518): A, dorsal view; B, ventral view.

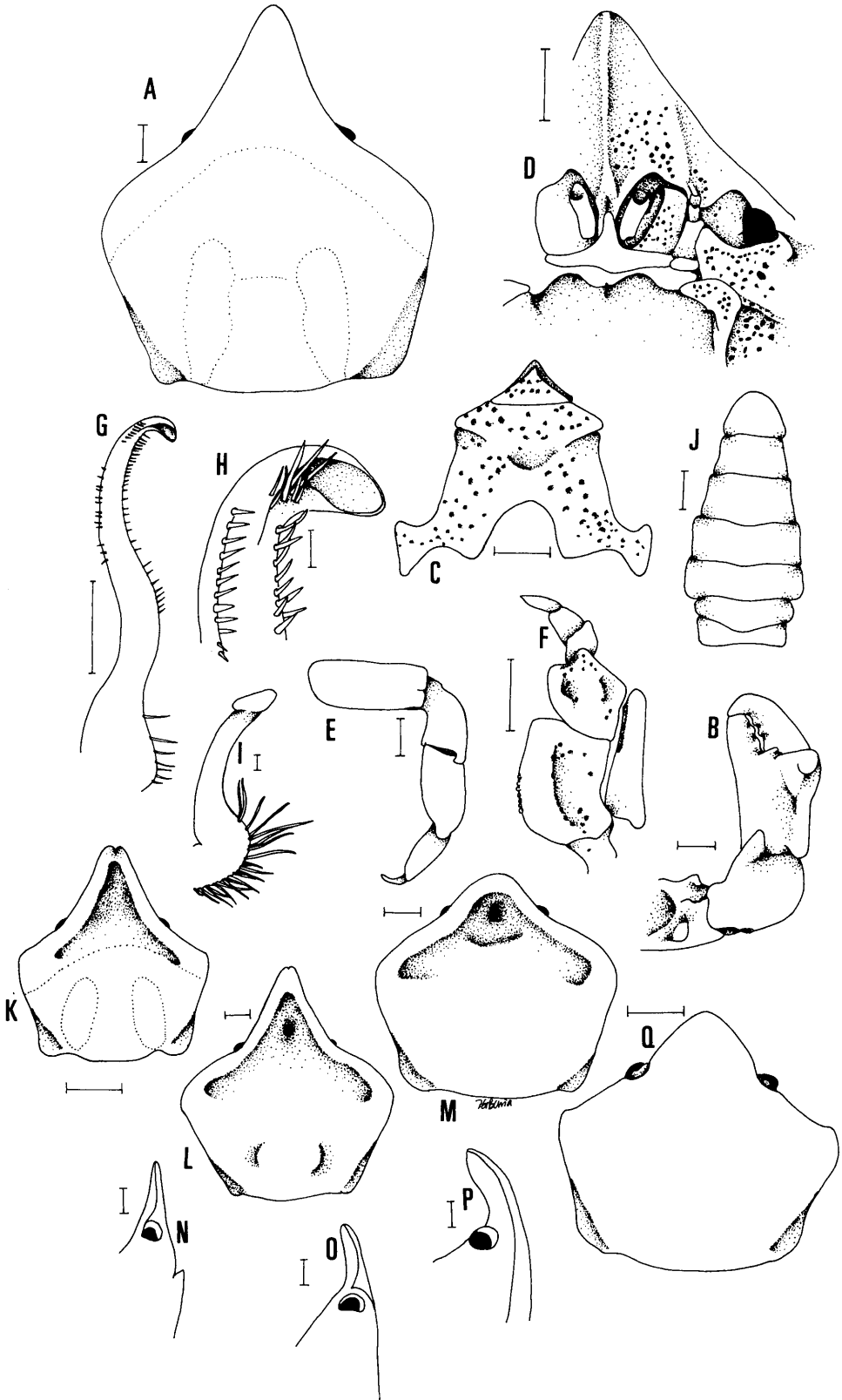
Reef, reef flat, on *Echinothrix* sp., Rawley Expedition, 24 July 1982; 1 ♀ (ovigerous) (USNM), on sea urchin in lagoon, under cave, on sand, Fairfax Island, Australian South Pacific Territory, collected by Booth, September 1966. Solomon Islands: 4 ♂♂ (4.5 × 3.7 mm, 5.4 × 4.8 mm, 6.6 × 6.9 mm, and 10.4 × 9.0 mm), 1 ♀ (MNHN-B 25657), Florida Island, collected by T. M. Iliffe and S. Sarbu, 12 August 1988. Papua New Guinea: 1 ♀ (ZRC 1998.51), Laing Island, on *Diadema setosum*, collected by D. Vandenspiegel, 1988. French Polynesia: 1 ♀ (12.8 × 11.2 mm) (holotype of *Eumedon convictor* Bouvier and Seurat, MNHN MP-B 24733), Hao Island, Tuamotu Archipelago, French Polynesia, collected by V. Noir, 1904; 4 ♀♀ (13.0 × 11.2 mm, 14.0 × 13.0 mm, 11.8 × 10.5 mm, and 13.5 × 12.2 mm) (MNHN B24734–35), Hao Island, Tuamotu Archipelago, French Polynesia, lagoon, 1990s; 1 ♂, 1 ♀ (USNM 95108), station 2246, commensal on the anal plate region of “banded spined poisonous sea urchin,” from pockets in inner reef, only near lagoon edge of reef in transect area at night, north end off Ngarumaoa Island, Raroia Atoll, Tuamotu Islands, collected by J. P. E. Morrison, 2 September 1952. Hawaiian Islands: 2 ♂♂ (SMF TS64), Waikiki, Oahu, on *Echinothrix diadema*, collected by T. Sakai, October 1960; 3 ♂♂, 5 ♀♀ (ZRC 1997.154–161), Oahu, on *Echinothrix calamaris*, collected by P. Castro; 1 ♀ (WAM 92–93), off Eea Beach, near Pearl Harbor, Oahu, 28 m, collected by B. R. Wilson, R. V. Pele, 5 July 1964; 4 ♀♀ (WAM 93–93), off Honolulu, dredged, 27–40 m, collected by T. Richert, February–March 1962; 1 ♀ (WAM 89–93), off Oahu, 37–110 m, collected by T. Richert, late 1963; 1 ♂, 3 ♀♀ (WAM 94–93), collected by T. Richert, May 1963; 1 ♂ (BPBM 1973.237), with spines of *Echinothrix diadema*, Hanauma Bay, Oahu, collected by Hawaii Marine Laboratory; 1 ♂, 1 juvenile ♀ (BPBM 1973.227), from *Echinothrix diadema*, Waikiki, Oahu, 40 feet (12.2 m) depth, collected by Hawaii Marine Laboratory; 1 ♂ (BPBM 1973.227), from *Echinothrix diadema*, Waikiki, Oahu, 40 feet (12.2 m) depth, collected by Hawaii Marine Laboratory; 1 ♂, 1 juvenile ♀ (BPBM 1973.227), from anal region of *Echinothrix diadema*, off Waikiki, Oahu, 40 feet (12.2 m) depth, collected by L. Trott, Hawaii Marine Laboratory; 1 ♀ (BPBM 1973.227), Waikiki, Oahu, 40 feet (12.2 m) depth, collected by L. Trott, Hawaii Marine Laboratory; 2 ♀♀ (BPBM 1973.227), on *Echinothrix calamaris*, Rabbit Island, Oahu, collected 23 March 1963; 1 ♀ (BPBM S10304, 1979.309), under rock, commensal on *Diadema*, Waikiki, Oahu, 80 feet (24.4 m) depth, collected by E. Chave, February 1983; 5 ♂♂ (largest 15.5 × 16.0 mm) (BPBM 5300) (as *Echinoecus rathbunae*), off Fort Du Russy, Oahu, in 25 feet (7.6 m) water, collected by Tinker and Smith, 6 September 1947; 1 ♂ (dried) (BPBM 10495, 1973.227), Oahu; 1 ♀ (BPBM uncatalogued); 1 ♀ (USNM), Waikiki Beach, Honolulu, Oahu, collected by F. E. Lewis, 11 September 1939; 1 ♂ (USNM 29740), station 4147, 26 fathoms (47.5 m), vicinity of Bird Island, collected by RV *Albatross*.

Description.—Carapace oval, rostrum elongate, center of rostrum sometimes depressed; regions poorly defined; surfaces of carapace, chelipeds, and ambulatory legs smooth to punctate, without granules; dorsal surface of carapace glabrous, never covered with pubescence. Antero- and posterolateral margin clearly demarcated, anterolateral margin

rounded. Antennules folding very obliquely, 60–70° from horizontal. Antenna free, not filling orbital hiatus, reaching into orbit; antennal basal segment rectangular; second antennal segment short, length subequal to width. Anterior surface of epistome not depressed; posterior margin entire with 2 fused truncate median lobes. Pterygostomial, subhepatic, and suborbital regions heavily pitted. Third maxilliped quadrate; ischium rectangular, median oblique sulcus shallow; merus squarish; exopod just reaching antero-external edge of merus. Anterior thoracic sternites relatively narrow; sutures between sternites 1 and 2 indistinct, 2 and 3 distinct, shallow; between 3 and 4 interrupted medially; lateral clefts small. Abdomen 7 segmented, sutures for all segments visible. Chelipeds smooth to punctate; carpus with 1 sharp inner distal spine, merus with single inner and outer distal teeth; chela short, stout; fingers smooth, not carinate, pollex not bent downward. Ambulatory leg segments smooth, subcylindrical; anterior margin of ambulatory merus rounded, distal edge occasionally pointed in smaller specimens; merus subcristate; dactylus of first leg not longer than those on other legs. G1 long, slender.

Sexual Dimorphism.—Males and small females have a relatively longer rostrum. Adult females are generally much larger than males. The rostrums of large females bend downward and become smaller in relation to the carapace, which enlarges and becomes bulbous (Figs. 2K–P). The carapace of males often has white markings (Fig. 1).

Remarks.—The taxonomy of this species is one of striking coincidences. The specific name *pentagonus* has been used three times, all independently for the same species of crab but under three separate generic names. Alphonse Milne Edwards (1879) first used the name for a crab from Mauritius under the genus *Eumedon* (sic H. Milne Edwards, 1834, see earlier). Rathbun (1894) subsequently established a new genus and species, *Echinoecus pentagonus*, for a specimen from Japan. Klunzinger (1906) then established *Liomedon pentagonus* for a specimen from the Red Sea. To confuse matters further, White (1847) described a very different genus and species of eumedonid, *Gonatonotus pentagonus*, from Borneo. Not surprisingly, some authors confused these names in different combinations.



As suggested by Nobili (1907), Balss (1922), Monod (1938), and Serène *et al.* (1958), *Liomedon pentagonus* Klunzinger, 1906, is regarded as a subjective junior synonym of *Echinoecus pentagonus*. Klunzinger's figure clearly supports this, as do the Red Sea (type locality of *L. pentagonus*) specimens examined in the present study.

Bouvier and Seurat (1905) described a new species, *Eumedon convictor*, but made the same mistake as A. Milne Edwards (1879) by using the generic name *Eumedon*, which is a vernacular name established by H. Milne Edwards (1834) for a different genus, *Eumedonus*. Subsequent workers (Laurie, 1915; Clark, 1950; Tweedie, 1950; Holthuis, 1953; Morrison, 1954, and Yang, 1979) corrected the spelling to *Eumedonus* (but not *Eumedonus* H. Milne Edwards, 1834, as defined here) when referring to this species. The type specimen of *E. convictor* was examined together with several specimens from French Polynesia. They are conspecific with the type of *Echinoecus pentagonus* (A. Milne Edwards). Balss (1922) and Serène *et al.* (1958) had in fact already argued that *E. convictor* is a junior synonym of *Echinoecus*.

The characters of the type specimens of *Eumedonus petiti* Gravier, 1922, do not deviate from the definition of *Echinoecus pentagonus* sensu stricto. Therefore, *E. petiti* is regarded as a subjective junior synonym of *Echinoecus pentagonus*.

The specimen reported by Balss (1922) as *Eumedonus pentagonus* is probably referable to *Echinoecus pentagonus* (A. Milne Edwards, 1879), since it was collected from the Ogasawara (= Bonin) Islands.

Miyake (1939) established two species, *Echinoecus rathbunae* and *Echinoecus klunzingeri*. The reason for establishing *E. rathbunae* was based on the fact that the eyes of his specimen (collected from the Ogasawara Islands) were concealed and the anterior mar-

gin of the ambulatory merus was extended distally into a spine. Since the Ogasawara Islands is the type locality of *Echinoecus pentagonus* Rathbun, 1894, Miyake (1939) concluded that *Echinoecus pentagonus* Rathbun, 1894, is a valid taxon, but must be regarded as distinct from *Echinoecus pentagonus* (A. Milne Edwards, 1879). He thus proposed *E. rathbunae* as a replacement name for *Echinoecus pentagonus* Rathbun, 1894. We find that the two characters that Miyake (1939) used can be easily explained by intraspecific variation. The carapaces of the larger females of *Echinoecus pentagonus* (A. Milne Edwards, 1879) have a tendency to become bulbous, thus covering the eyes (see Figs. 2N–P) and the distal edge of the anterior margin of the ambulatory leg does not develop into a spine. Miyake's specimen from the Ogasawara Islands is a much larger female (11.0 × 9.7 mm) than the type of A. Milne Edwards (1879) (8.5 × 7.9 mm). Therefore, *E. rathbunae* is here regarded as a subjective junior synonym of *E. pentagonus* (A. Milne Edwards, 1879). As discussed earlier, this is also the case for his *E. rathbunae convictor* (Bouvier and Seurat, 1905).

Echinoecus klunzingeri (Miyake, 1939) was established on the basis that there were no color markings and no grooves on the carapace. These features again are easily accounted for by intraspecific variation. As the females of *Echinoecus pentagonus* (A. Milne Edwards, 1879) become larger, they tend to lose their color markings and become dull maroon red in color and the carapace becomes bulbous. Thus, the present study agrees with Serène *et al.* (1958) in regarding *Echinoecus klunzingeri* (Miyake, 1939) as a subjective junior synonym of *Echinoecus pentagonus* (A. Milne Edwards, 1879).

Although the general carapace morphology is relatively constant, the shape of the rostrum varies at times, from very long to very short

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Fig. 2. *Echinoecus pentagonus* (A. Milne Edwards, 1879), A–J, male 11.7 × 9.7 mm, Mahe, Seychelles (RMNH 42518): A, dorsal view of carapace; B, posterodorsal view of right cheliped; C, sternum; D, face of carapace; E, fourth right ambulatory leg; F, left third maxilliped; G, left G1; H, distal tip of left G1; I, left G2; J, abdomen; K, male 4.5 × 3.7 mm, Solomon Islands (MNHN-B 25657); L, male, 10.4 × 9.0 mm, Solomon Islands (MNHN-B 25657); M, male, 6.6 × 6.9 mm, Solomon Islands (MNHN-B 25657); N, male, cw 7.7 mm (ZRC 1997.154–161); O, male, 11.4 × 10.3 mm, Hawaii (ZRC 1996.154–161); P, male 15.5 × 15 mm, Hawaii (ZRC 1997.154–161); Q, *Echinoecus nipponicus* Miyake, 1939, male 5.1 × 5.5 mm, Manuruazu, Japan (NSMT). Scales for A–G, I–Q = 1.0 mm; for H = 0.1 mm.

as seen in the case of some specimens from Florida Island (Solomons) (Figs. 2K–M). Females, which live inside the rectum of their sea urchin host, have a very short rostrum and a bulbous carapace. In larger specimens, the eyes are also more hidden (Figs. 2O, P) than in smaller specimens (Fig. 2N). The rostrum is somewhat more anteriorly inclined in certain specimens as compared to others (Figs. 2P versus 2N). This again is merely individual variation. The lateral teeth are also more pronounced in smaller specimens (Fig. 2N). Some specimens, especially large females, lack color markings, while others, particularly males, have two vertical white bands on the carapace (Fig. 1A). The G1 structure is fairly constant within the species (Figs. 2G, H, 4H).

Larvae.—The larvae were first reported by Castro (1971) and the larval development (first zoea to megalopa) was described by Van Dover *et al.* (1986).

Host Records.—Diadematidae: *Diadema savigni* (Michelin), *D. setosum* (Leske), *Echinothrix calamaris* (Pallas), *Echinothrix diadema* (Linnaeus); Echinometridae: *Heterocentrotus mammillatus* (Linnaeus); and Strongylocentrotidae: *Pseudocentrotus depressus* (Agassiz).

Distribution.—This is a very wide ranging Indo-West Pacific species, and has been recorded from the Red Sea and East Africa to the Hawaiian Islands and French Polynesia. It has, however, yet to be reported from within the Sunda Shelf.

Echinoecus nipponicus Miyake, 1939
Figs. 2Q, 3, 4A–G

Echinoecus petiti nipponicus Miyake, 1939: 86, 88 [in key], 90, text-figs. 1B, 2B, 3B [type locality Okinoshima Island, Japan]; Serène *et al.*, 1958: 149, 151, 152, 156, 158 (part) (note only).

Echinoecus petiti nipponensis—Miyake *et al.*, 1962: 128.

Echinoecus pentagonus—Sakai, 1960: 53, pl. 26: fig. 5 [color plate] [list only]; Sakai, 1965: 102, pl. 46: fig. 3 [color plate] [volume in English], 42 [volume in Japanese] [Sagami Bay and Izu Peninsula, Honshu island, Japan]; Takeda, 1975: 23, 130 [color photographs] [list only]; Sakai, 1976: 295 [volume in English], 178 [volume in Japanese], pl. 100: fig. 1 [color plate] [Sagami Bay, Izu and Kii peninsulas, Honshu island, Japan]; Sakai, 1980: 3 [color plate], 227 [list only]; Takeda, 1982: 136, fig. 402 [color plate; fide Sakai, 1976] [list only]; Miyake, 1983: 55, 213, pl. 19: fig. 3 [color photograph] [list only]; Masuda *et al.*, 1986: 141 [color photograph] [list only]; Takeda 1992: 2–287 [list only] [not *Echinoecus pentagonus* (A. Milne Edwards, 1879)].

Eumedoncus pentagonus—Sakai, 1936: 18, 113, pl. 30: fig. 2 [color plate] [Honshu Island, Japan]; Miyake, 1937: 29, fig. 3 [Danjo Island, Japan]; Monod, 1938: 111, 112 [note only]; Sakai, 1938: 348 [in key], 349, 360, pl. 33: fig. 3. [color plate] [Honshu Island, Japan]; Sakai, 1940: 30 [list only] [not *Eumedoncus pentagonus* A. Milne Edwards, 1879].

Material Examined.—Japan: Holotype: ♂ (6.4 × 6.7 mm) (KMNH 5775), Okino-Shima Island, 34°15'N, 130°06'E, Okinoshima Expedition II, collected 19–29 May 1933; paratypes: 1 ♀ (allotype) (KMNH 5776), 2 ♀♀ (KMNH 5777–8), same data as holotype; 1 juvenile ♀ (ZRC 1997.151), Kushimoto, on *Acanthocidaris crassispina*, collected by S. Nagai, June 1991, 1 ♂ (5.1 × 5.5 mm), 2 ♀♀ (NSMT), Manazuru, on *Acanthocidaris crassispina*, collected by H. Suzuki, 25 April 1970; 1 ♂ (4.5 × 4.7 mm), 1 ♀ (NSMT), Kushimoto, Wakayama Prefecture, associated with *Pseudocentrotus depressus*, collected 4 November 1973; 1 ♂ (6.2 × 6.4 mm) (ZRC 1997.152), at the back of Danish Experimental Station, Nagasaki University, Nomozaki-cho, Nagasaki Prefecture, on *Pseudocentrotus depressus*, collected by T. Inui, 8 December 1975.

Diagnosis.—Carapace slightly broader than long; rostrum short, broad and triangular; regions poorly defined; surfaces of carapace, chelipeds, and ambulatory legs smooth to punctate, without granules. Antero- and posterolateral margin of carapace clearly demarcated by small tooth. Subhepatic region mildly pitted. Anterior margin of ambulatory merus extending into small tooth distally. Anterior thoracic sternites relatively broad; surface smooth. G1 short, stout.

Sexual Dimorphism.—Not known.

Remarks.—Miyake (1939) established a new subspecies, *Echinoecus petiti nipponicus*, from Japan. Serène *et al.* (1958) synonymized it under *E. pentagonus* (A. Milne Edwards, 1879) stating that it merely represented variation within the species. The examination of a good series of specimens from Japan, including the types, however, shows that *E. petiti nipponicus* is, in fact, a valid taxon. *Echinoecus petiti* Gravier, 1922, *sensu stricto*, however, is a synonym of *E. pentagonus* (for reasons, see *E. pentagonus*).

When comparing specimens of similar sizes, *E. nipponicus* differs from *E. pentagonus* in having (1) a much shorter and broader rostrum (Figs. 2A, Q), (2) an anterolateral angle marked with a small tooth (Figs. 2A, Q), (3) the anterior thoracic sternum proportionately broader and the surface not pitted (Figs. 4C, 2C), and (4) the G1 relatively stouter and shorter (Figs. 4B, H). The present specimens agree well with the type

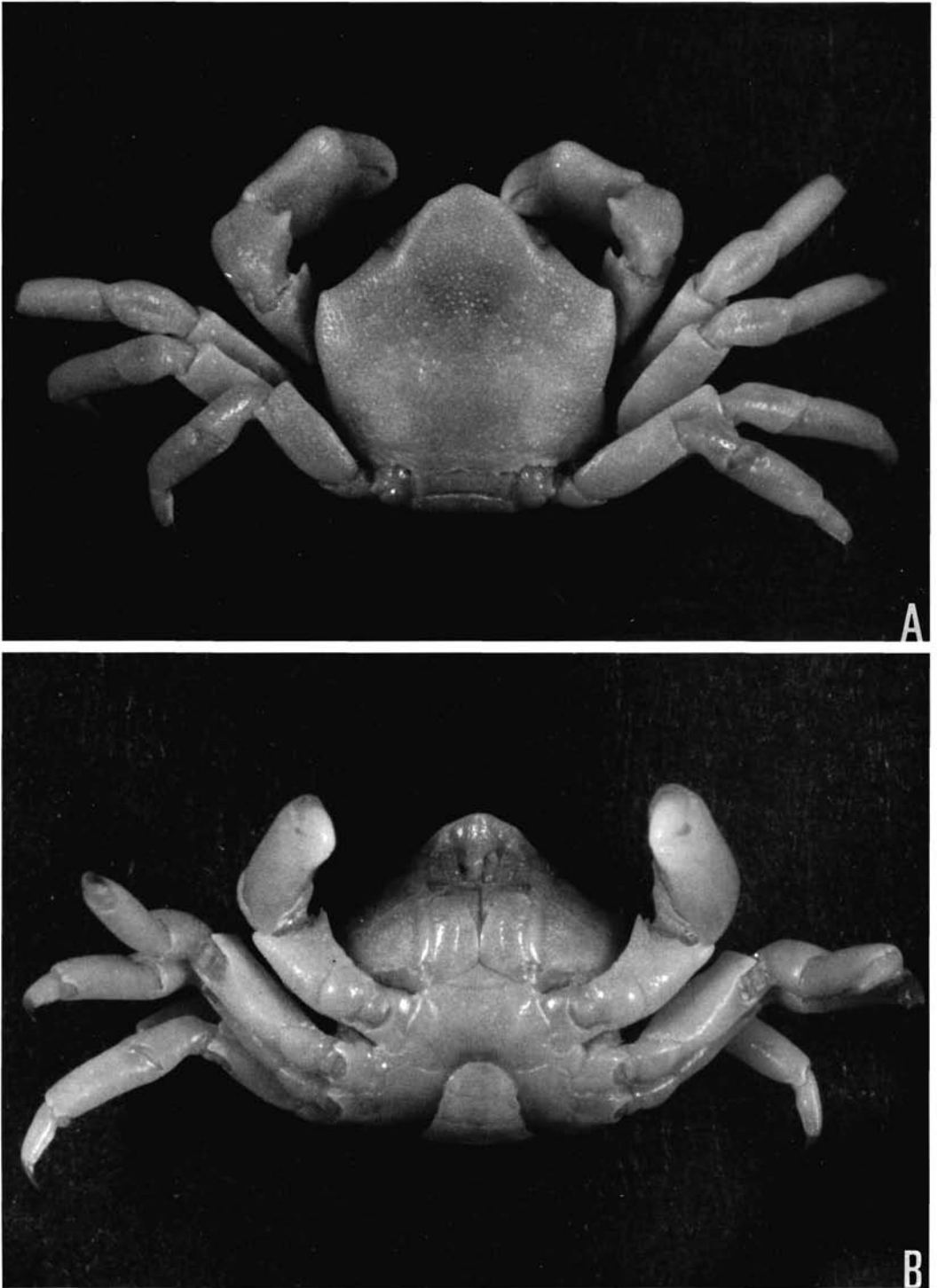
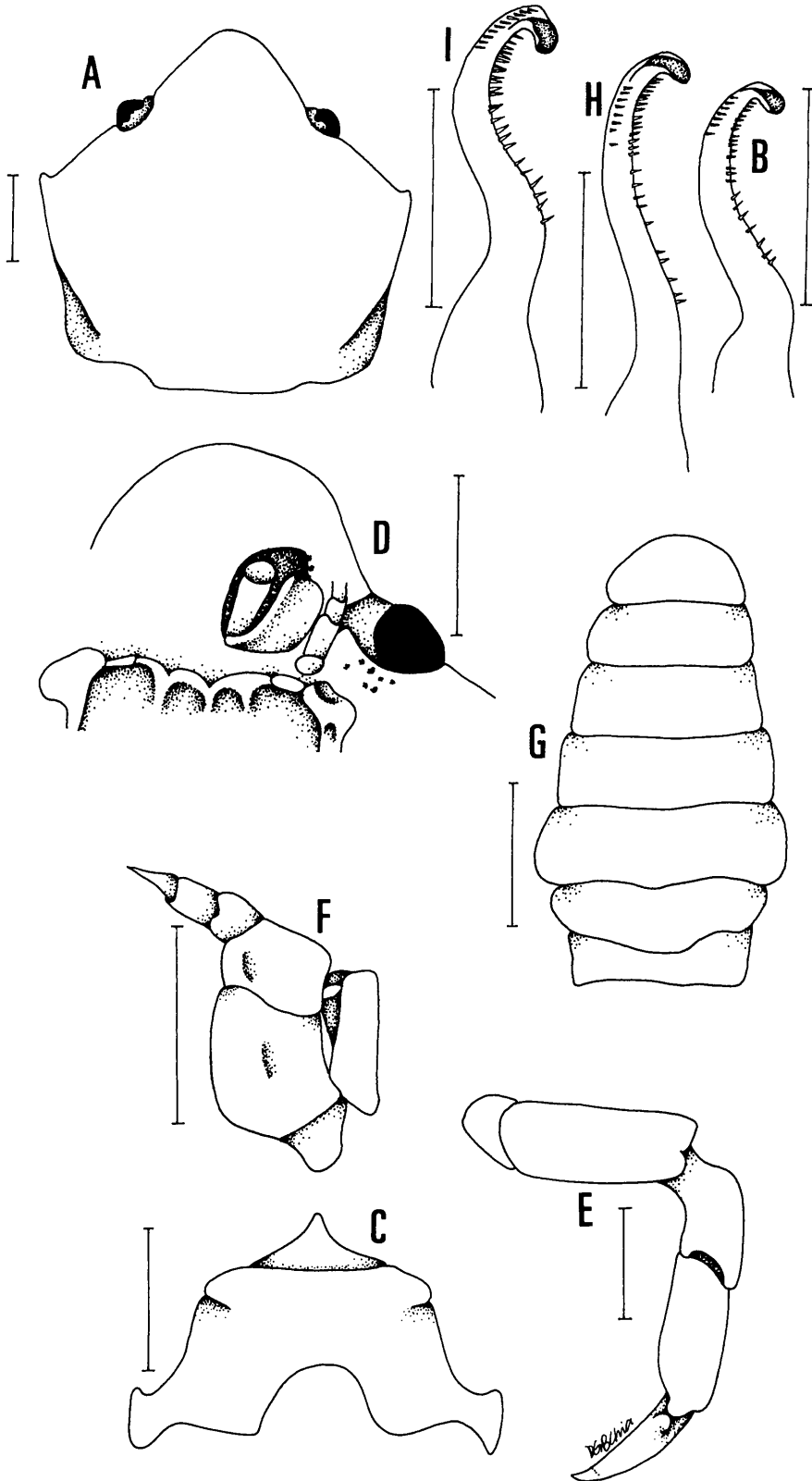


Fig. 3. *Echinoecus nipponicus* Miyake, 1939. Male, 5.1 × 5.5 mm, Manuruza, Japan (NSMT): A, dorsal view; B, ventral view.



specimens of Miyake (1939). Although some smaller specimens of *E. pentagonus* occasionally have a small anterolateral tooth and may have a short rostrum (see Fig. 4K, M), they nevertheless clearly differ from *E. nipponicus* in the anterior thoracic sternum and G1 structures.

From the illustrations and descriptions, we believe that the specimens reported by Sakai (1936, 1938, 1960, 1965, 1976, 1980), Takeda (1975, 1982, 1992), Masuda *et al.* (1986), and Miyake (1937, 1983) are *E. nipponicus*. Illustrations and descriptions by some Japanese authors, however, contain insufficient information for an accurate determination of their respective species. These records have been placed in the "Indeterminate Records" section.

With its short broad rostrum, squarish carapace form, and relatively stouter G1, *E. nipponicus* is more closely related to *E. sculptus* (Ward, 1934) than to *E. pentagonus*. For differences between *E. nipponicus* and *E. sculptus*, see comments on that species.

In contrast to *E. pentagonus*, where females invade the rectum of their sea urchin hosts (Castro, 1971), *E. nipponicus* always lives on the external surface of sea urchins.

Larvae.—Not known.

Host Records.—Echinometridae: *Heliocidaridaris* (= *Acanthocidaridaris*) *crassispina* (Agassiz), and Strongylocentrotidae: *Pseudocentrotus depressus* (Agassiz).

Distribution.—Known only from Japan.

***Echinoecus sculptus* (Ward, 1934),
new combination
Figs. 4I, 5, 6**

Proechinoecus sculptus Ward, 1934: 5, 7, figs. 5, 5a [type locality Christmas Island, Indian Ocean]; Serène *et al.*, 1958: 240 [list only]; Serène and Romimohtarto, 1963: 2, figs. 1A, 2, pl. I: figs. A, B [Christmas Island]; Serène, 1968: 63 [list only]; Yang, 1979: 12 [Christmas Island]; Števíč *et al.*, 1988: 1312 [list only].

Eumedonus sculptus—Buitendijk, 1950: 74 [Christmas Island].

Material Examined—Paratypes: 7 ♂♂ (largest 4.7 × 5.3 mm, 4.8 × 4.8 mm), 17 ♀♀ (largest 5.0 × 5.7 mm) (ZRC

1965.10.19.83–92), 1 ♂, 1 ♀ (USNM 78292), Christmas Island, under *Colobocentrotus atratus*, collected by M. Tweedie, September 1932. Others: Christmas Island: 1 ♂ (ZRC 1970.8.25.1), Christmas Island, under *Colobocentrotus atratus*, collected by M. Tweedie, September 1932; 2 ♀♀ (WAM 109–93), mouth of N°5 Dale, on *Colobocentrotus*, splash and surge at low tide, collected by S. Slacksmith and A. Paterson, 1 October 1969; 1 ♂ (WAM 640–88), on urchin, collected by H. Yorkston, July 1988; 2 ♂♂, 2 ♀♀ (WAM 99–93), north point, collected by Powells, August 1961; 1 ♀ (WAM 91–93), Dolly Beach, constant splash at low tide, collected by S. Slacksmith and A. Paterson, 27 and 28 September 1969; 1 ♂, 3 ♀♀ (WAM 106–93), northeast point, near Davis House, under sea urchin *Colobocentrotus* sp., collected by D. Powell, 14 February 1978; 2 ♂♂, 4 ♀♀ (RMNH 5467), commensal with *Colobocentrotus atratus*, 1940.

Diagnosis.—Carapace slightly broader than long, rostrum short; frontal margin trilobed; regions poorly defined; surface of carapace highly pitted and rugose, surfaces of che-lipeds and ambulatory legs smooth. Antero- and posterolateral margins clearly demarcated by small tooth. Subhepatic region mildly pitted. Anterior thoracic sternites relatively broad, surfaces mildly pitted. G1 short, stout.

Sexual Dimorphism.—The carapaces of females are highly pitted with fossae of varying sizes and depths (Figs. 6K, L).

Remarks.—Buitendijk (1950) reported on some specimens that were identified as *Eumedonus sculptus* (RMNH 5467). She had synonymized both *Echinoecus* and *Gonatonotus* under *Eumedonus*. These three genera are considered as separate taxa in the present study and her specimens are reidentified as *Echinoecus sculptus* (Ward, 1934), new combination.

The numerous specimens from Christmas Island that were examined agree very well with the paratypes examined. *Echinoecus sculptus* differs from its nearest congener, *E. nipponicus*, in having a trilobed frontal margin, rugose carapace, strong sexual dimorphism, and a more pitted sternum (Figs. 6A, C, K, L).

Larvae.—Not known.

Host Records.—Echinometridae: *Colobocentrotus atratus* (Linnaeus).

Fig. 4. A–G, *Echinoecus nipponicus* Miyake, 1939, male 4.5 × 4.7 mm, Wakayama, Japan (NSMT): A, dorsal view of carapace; B, left G1; C, sternum; D, face of carapace; E, fourth right ambulatory leg; F, left third maxilliped; G, abdomen; H, *Echinoecus pentagonus* (A. Milne Edwards, 1879), male 5.4 × 4.8 mm, Solomon Islands (MNHN-B 25657), left G1; I, *Echinoecus sculptus* (Ward, 1934), new combination, paratype, male, 4.8 × 4.8 mm, Christmas Island (ZRC 1965.10.19.83), left G1. Scale = 1.0 mm.



Fig. 5. *Echinoecus sculptus* (Ward, 1934), new combination, paratype male, 4.7 × 5.3 mm, Christmas Island (ZRC 1965.10.19.83): A, dorsal view; B, ventral view.

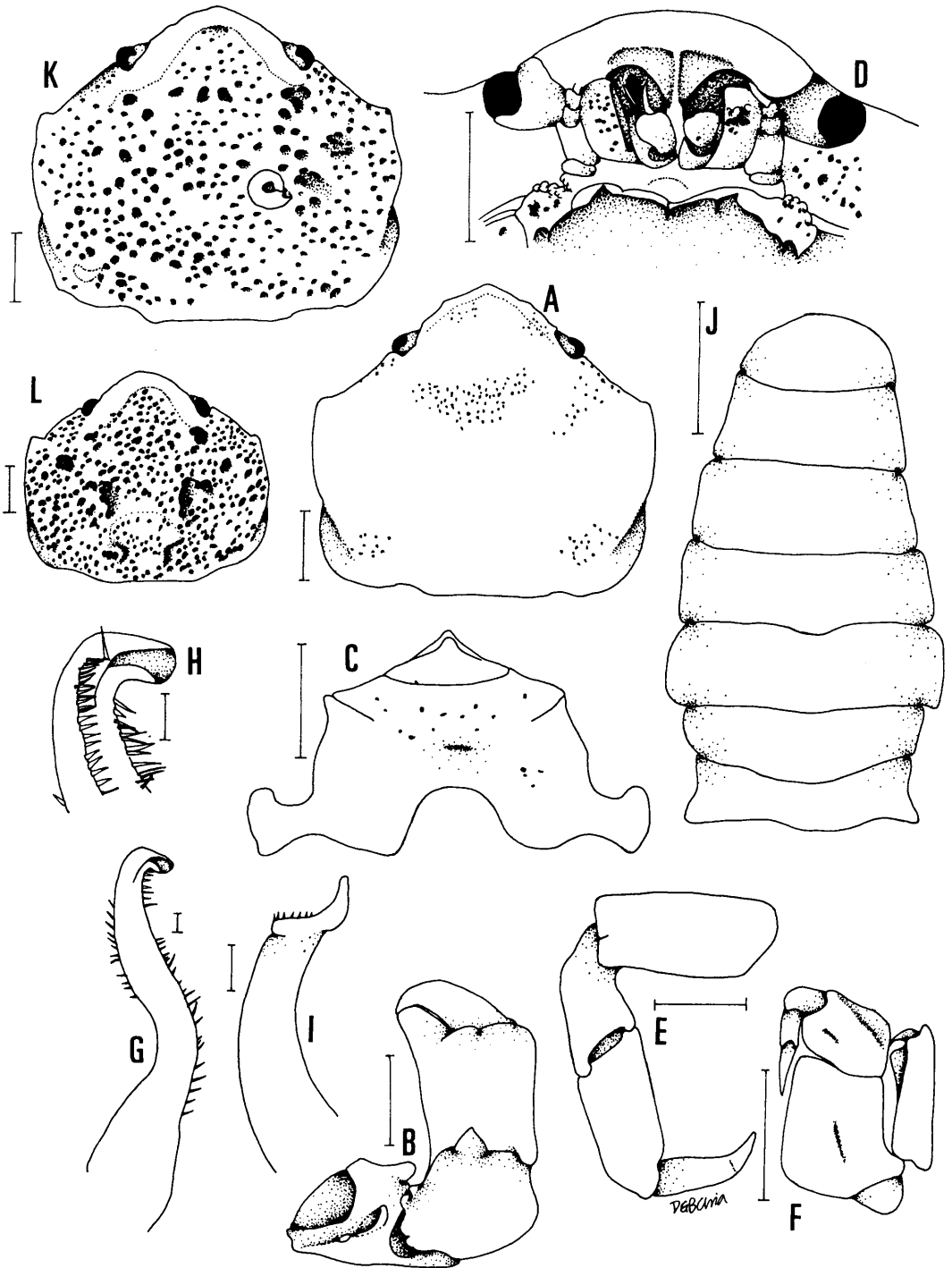


Fig. 6. *Echinoecus sculptus* (Ward, 1934), new combination, A–J, paratype, male 4.7 × 5.3 mm, Christmas Island (ZRC 1965.10.19.83); K, paratype, female, 5.0 × 5.7 mm (ZRC 1965.10.19.84); L, paratype, female, 5.0 × 5.7 mm (ZRC 1965.10.19.85). A, K, L, dorsal view of carapace; B, posterodorsal view of right cheliped; C, sternum; D, face of carapace; E, fourth left ambulatory leg; F, left third maxilliped; G, left G1; H, distal tip of left G1; I, left G2; J, abdomen. Scales for A–G, I–L = 1.0 mm; for H 0.1 mm.

Distribution.—Known only from Christmas Island, eastern Indian Ocean.

Indeterminate Records

The following list includes records of specimens encountered in this study whose identities cannot be ascertained, since specimens were not available for examination. Most of the Japanese records are probably *E. nipponicus*.

- Echinoecus pentagonus*—Sakai, 1956: 25 [as "*E. pentagonus* (Rathbun)"; appendix list] [list only].
- Echinoecus pentagonus*—Suzuki and Kurata, 1967: 98 [Izu Islands, Japan].
- Echinoecus pentagonus*—Kayama, 1970: 8, figs. 1–6 [Yoroto Island, Ryukyu Islands, Japan].
- Echinoecus pentagonus*—Nishimura and Suzuki, 1971: 112 [fig.] [list only].
- Echinoecus pentagonus*—Suzuki and Takeda, 1974: 294 [Izu Peninsula, Honshu Island, Japan].
- Echinoecus pentagonus*—Watabe, 1974: 139 [Sagami Bay, Honshu Island, Japan].
- Echinoecus pentagonus*—Takeda and Miyake, 1976: 107 [list only].
- Echinoecus pentagonus*—Miyake and Takeda, 1978: 37 [Amakusa Island, Japan].
- Echinoecus pentagonus*—Imanaka *et al.*, 1984: 63, 71 [Honshu Island, Japan].
- Echinoecus pentagonus*—Kim and Chang, 1985: 50, 57, 41, fig. 4 [Cheju Island, South Korea].
- Echinoecus pentagonus*—Yamaguchi *et al.*, 1987: 17 [Amakusa Islands, Japan].
- Echinoecus pentagonus*—Takeda, 1994: 246 [Japan].
- Echinoecus pentagonus*—Anonymous, 1992: 8 (color photograph) [Japan?].

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LITERATURE CITED

- Anonymous. 1974. On zoological surveys of the South China Sea.—*Acta Zoologica Sinica* 20: 113–130. [In Chinese.]
- . 1992. Izu Oceanic Park (I.O.P.).—*Diving News* 3: 1–8.
- Balss, H. 1922. Die Dromiaceen, Oxystomen und Parthenopiden. *Ostasiatische Decapoden*, III.—*Archiv für Naturgeschichte* 88(A)(3): 104–140.
- . 1924. Die Oxyrhynchen und Schlussteil (Geographische Übersicht der Decapoden Japans). *Ostasiatische Decapoden*, V.—*Archiv für Naturgeschichte* 90(A)(5): 20–84.
- . 1957. Decapoda, VIII: Systematik.—*In*: H. G. Bronns, *Klassen und Ordnungen des Tierreichs*.—Akademische Verlagsgesellschaft, Leipzig, (5)(1)7(12): 1131–1199.
- Barnard, K. H. 1954. Notes sur une collection de Crustacés Décapodes de la région malgache.—*Mémoires de l'Institut Scientifique de Madagascar* A(9): 95–104.
- . 1955. Additions to the fauna-list of South African Crustacea and Pycnogonida.—*Annals of the South African Museum* 43: 1–107.
- Bouvier, E.-L., and G. Seurat. 1905. *Eumedon convictor*, crabe commensal d'un oursin.—*Comptes Rendus des Séances de l'Académie des Sciences* 140: 629–631.
- Buitendijk, A. M. 1950. On a small collection of Decapoda Brachyura, chiefly Dromiidae and Oxyrhyncha, from the neighbourhood of Singapore.—*Bulletin of the Raffles Museum* 21: 59–82.
- Castro, P. 1971. Nutritional aspects of the symbiosis between *Echinoecus pentagonus* and its host in Hawaii, *Echinothrix calamaris*.—*In*: *Aspects of the biology of symbiosis*. T. C. Cheng, ed. Pp. 229–247. University Park Press, Baltimore, Maryland.
- . 1978. Settlement and habitat selection in the larvae of *Echinoecus pentagonus* (A. Milne Edwards), a brachyuran crab symbiotic with sea urchins.—*Journal of Experimental Marine Biology and Ecology* 34: 259–270.
- Chen, H. L. 1975. Studies on the crabs of Xisha Islands I. Guangdong Province, China.—*Studia Marina Sinica* 10: 157–179.
- Clark, A. H. 1950. Echinoderms from the Cocos-Keeling Islands.—*Bulletin of the Raffles Museum* 22: 53–67.
- Dai, A., and S. Yang. 1991. *Crabs of the China seas*.—China Ocean Press, Beijing, China, and Springer-Verlag, Berlin, Germany. Pp. 1–21, 1–608.
- , S. Yang, Y. Song, and G. Chen, 1986. *Crabs of the China seas*.—China Ocean Press, Beijing, China. Pp. 1–17, 1–642. [In Chinese.]
- Flipse, H. J. 1930. Oxyrhyncha [sic]: Parthenopidae. Die Decapoda Brachyura der Siboga-Expedition, VI.—*Siboga-Expeditie 39c2*(112): 1–96. [University of Amsterdam edition with added introduction in Dutch and different pagination.]
- Gravier, C. 1922. Sur un nouveau crabe (*Euymedonus Peitii* nov. sp.) commensal d'un oursin de Tulear (Madagascar).—*Bulletin de Muséum National d'Histoire Naturelle* 28: 484–486.
- Guinot, D. 1966. La faune carcinologique (Crustacea Brachyura) de l'Océan Indien occidental et de la Mer Rouge. Catalogue, remarques biogéographiques et bibliographie.—*Mémoires de l'Institut Fondamental d'Afrique Noire* 77: 235–352.
- Holthuis, L. B. 1953. Enumeration of the decapod and stomatopod Crustacea from Pacific coral islands.—*Atoll Research Bulletin* 24: 1–66.
- Imanaka, T., Y. Sasada, H. Suzuki, S. Segawa, and T. Masuda. 1984. Crustacean decapod fauna in Kominato and adjacent waters middle Honshu: a provisional list.—*Journal of the Tokyo University of Fisheries* 71: 45–74.
- Kayama, Y. 1970. Crabs from Yoroto Island and a crab living in a sea urchin, *Diadema setosum*.—*Kyano Oikos, Marine Ecological Researching Society of Kagoshima University* 10: 7–14. [In Japanese.]
- Kim, H. S., and C. Y. Chang. 1985. The brachyuran crabs of Cheju Island, Korea (Crustacea: Decapoda).—*Korean Journal of Systematic Zoology* 1: 41–60.
- Klunzinger, C. B. 1906. Die Spitz- und Spitzmundkrabben (Oxyrhyncha und Oxystomata) des Roten Meeres.—

- Verlag von Ferdinand Enke, Stuttgart, Germany. Pp. vii+91.
- . 1913. Die Rundkrabben (*Cyclometopa*) des Roten Meeres.—Abhandlungen der Kaiserlichen Leopoldinisch-Carolinischen Deutschen Akademie der Naturforscher 99: 97–402.
- Laurie, R. D. 1915. On the Brachyura. Reports on the marine biology of the Sudanese Red Sea, from collections made by Cyril Crossland, M.A., B. Sc., F.Z.S., XXI.—Journal of the Linnean Society of London, Zoology 31: 407–475.
- Masuda, H., K. Hayashi, H. Nakamura, and A. Kobayashi (editors). 1986. Marine invertebrates. Tokai University Press, Tokyo, Japan. Pp. 1–255. [In Japanese.]
- Mather, P., and I. Bennett (editors). 1984. A coral reef handbook. A guide to the fauna, flora and geology of Heron Island and adjacent reefs and cays, second edition.—Australian Coral Reef Society, Brisbane, Australia. Pp. 1–444. [Third edition published in 1993.]
- Michel, C. 1964. Check list of the Crustacea Brachyura (crabs) recorded from Mauritius.—Bulletin of the Mauritius Institute 6: 1–48.
- Milne Edwards, A. 1879. Description de quelques Crustacés nouveaux.—Bulletin de la Société philomatique Paris 7: 103–110.
- Milne Edwards, H. 1834. Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie et la classification des ces animaux 1: xxxv+468 pp. Atlas [1834, 1837, 1840]: 1–32, pls. 1–14, 14 bis, 15–25, 25 bis, 26–42.—Librairie Encyclopédique de Roret, Paris, France.
- Miyake, S. 1937. Brachyura of the Danjo Islands.—Biogeographica 2: 27–30. [In Japanese.]
- . 1939. Note on crabs of the genus *Echinoecus* Rathbun living commensally with echinoids (*Parthenopidae*, *Eumedoninae*).—Annotationes Zoologicae Japonenses 18: 83–94.
- . 1983. Brachyura (crabs). Japanese crustacean decapods and stomatopods in color 2: i–viii+1–277, pls. 1–64, unnumbered fig. First edition.—Hoikusha, Osaka, Japan. [In Japanese.]
- , and M. Takeda. 1978. Suborder Brachyura.—In: T. Kikuchi and S. Miyake, eds., Fauna and flora of the sea around the Amakusa Marine Biological Laboratory, Part II, Decapod Crustacea. Revised edition. Pp. 32–45.—Amakusa Marine Biological Laboratory, Kyushu University, Tomioka, Japan.
- , 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 6: 121–131.
- Monod, T. 1938. Decapoda Brachyura. Missión Robert Ph. Dollfus en Egypte, VIII.—Mémoires, Institut d'Egypte 37: 91–162.
- Mori, A., Y. Yanagisawa, Y. Fukuda, and P. K. L. Ng. 1991. Complete larval development of *Zebrida adamsii* White, 1847 (Decapoda: Brachyura), reared in the laboratory.—Journal of Crustacean Biology 11: 292–304.
- Morrison, J. P. E. 1954. Ecological notes on the mollusks and other animals of Raroia. Animal ecology of Raroia Atoll, Tuomotus, part 1.—Atoll Research Bulletin 34: 1–18.
- Mortensen, T. 1940. Aulodonta with additions to Vol. II (Lepidocentroidea and Stirodonta).—In: A monograph of the Echinoidea, Vol. 3(1): 1–370. C. A. Reitzel, Copenhagen, Denmark.
- Nagai, S., and K. Nomura. 1988. Crustacea (Brachyura). [The guide book of marine organisms of Okinawa] 7: 1–250. Shinsei Tosho, Okinawa, Japan. [In Japanese.]
- Nishimura, S., and K. Suzuki. 1971. Common seashore animals of Japan in color.—Hoikusha, Osaka, Japan. Pp. 1–196, pls. 1–64. [In Japanese.]
- Nobili, G. 1907. Ricerche sui crostacei della Polinesia. Decapodi, stomatopodi, anisopodi e isopodi.—Mémoire della Reale Accademia delle Scienze di Torino (2)57: 351–430.
- Rathbun, M. J. 1894. Notes on the crabs of the family Inachidae in the United States National Museum.—Proceedings of the United States National Museum 17: 43–75.
- . 1906. The Brachyura and Macrura of the Hawaiian Islands.—Bulletin of the United States Fisheries Commission 23: 827–930.
- Sakai, T. 1936. Crabs of Japan. 66 plates in life colours with descriptions.—Sanseido, Tokyo, Japan. Pp. 1–239, 1–12 [literature cited], 1–27 [bibliography and index], pls. 1–66. [Dated 1935 but published in 1936.]
- . 1938. Brachygnatha, Oxyrhyncha.—In: Studies on the crabs of Japan 3: 194–364. Yokendo, Tokyo, Japan.
- . 1940. Bio-geographic review on the distribution of crabs in Japanese waters.—Records of Oceanographic Works in Japan 11: 27–63.
- . 1956. Crabs.—Pp. 1–60 [list of Latin names], 1–224 [Japanese text], 1–4 [introduction, pls. 6.] Saito Press, Tokyo, Japan.
- . 1960. Order Decapoda, Suborder Brachyura.—In: K. Okada and T. Uchida, eds., Encyclopedia zoologica illustrated in colours 4: 8–87, pls. 14–43. Hokuryukan, Tokyo, Japan. [In Japanese.]
- . 1965. The crabs of Sagami Bay.—Pp. xvi+206 [English text], pp. 1–92 [Japanese text], pp. 1–32 [bibliography and indices], pls. 1–100. Maruzen, Tokyo, Japan.
- . 1976. Crabs of Japan and the adjacent seas.—Volume 1 [English]: Pp. xxix+773; volume 2 [Japanese]: pp. 1–461; volume 3 [plates]: pp. 1–61, pls. 1–251. Kodansha, Tokyo, Japan.
- . 1980. Crabs: their ecology and mystery.—Pp. 1–297. Kodansha, Tokyo, Japan. [In Japanese.]
- Sastry, D. R. K. 1977. On some crustacean associates of sea-urchins of the Andaman and Nicobar Islands.—Newsletter, Zoological Survey of India 3: 119–120.
- . 1981. On some crustacean associates of Echinoderms from the Bay of Bengal.—Records of the Zoological Survey of India 79: 19–30.
- Serène, R. 1968. The Brachyura of the Indo-West Pacific region.—In: Prodromus for a check list of the non-planctonic marine fauna of South East Asia.—Singapore National Academy of Science, Special Publication 1: 33–112.
- , and K. Romimohtarto. 1963. On some species of *Eumedoninae* from Indo-Malayan region.—Marine Research in Indonesia 6: 1–14.
- , T. V. Duc, and N. V. Luom. 1958. *Eumedoninae* du Viet-Nam (Crustacea) (avec un bibliographie de la sous-famille).—Treubia 24: 135–242.
- , K. Romimohtarto, and M. K. Moosa. 1974. The Hippidae and Brachyura collected by the Rumphius Expedition I.—Oseanologi in Indonesia 1: 17–26.
- Soltanpour-Gargari, A., R. Engelmann, and S. Wellershaus. 1989. Development and rearing of zoea larvae in Brachyura (Crustacea Decapoda): a bibliography.—Crustaceana, supplement 14: i–viii, 1–173.

- Števčić, Z., P. Castro, and R. H. Gore. 1988. Re-establishment of the Family Eumedonidae Dana, 1853 (Crustacea: Brachyura).—*Journal of Natural History* 22: 1301–1324.
- Suzuki, K., and Y. Kurata. 1967. On the carcinological fauna of the Izu-Oshima and its adjacent island.—*Researches on Crustacea* 3: 86–104.
- , and M. Takeda. 1974. On a parthenopid crab, *Zebrida adamsii* on the sea urchins from Suruga Bay, with a special reference to their parasitic relations.—*Bulletin of the National Science Museum, Tokyo* 17: 287–296.
- Takeda, M. 1975. Brachyura.—*In*: H. Utinomi, ed., *Aquatic invertebrates*.—*Gakken Chukosei Zukan* 9: 120–149 (figs. with Latin names), 188–331 (descriptions). First edition. Gakken, Tokyo, Japan. [In Japanese.] [Second edition in 1983 as “The aquatic lower animals of Japan” without changes.]
- . 1982. Keys to the Japanese and foreign crustaceans fully illustrated in colors.—Pp. i–vi, 1–285, 1–58 (keys). Hokuryukan, Tokyo, Japan.
- . 1992. Evolution and adaption in crabs.—*Shukan Asahi Hyakka Dubutsutai no Chikyu*, 69: 2–286–2–288. [In Japanese.]
- . 1994. Anomura and Brachyura.—*In*: *Seashore animals*. T. Okutani, ed. Yama-Kei Publisher, Tokyo, Japan. Pp. 221–264.
- , and S. Miyake. 1976. List of known species. Crabs of the Ogasawara Islands, I.—*Researches on Crustacea* 7: 101–115.
- Tweedie, M. W. F. 1950. The fauna of the Cocos-Keeling Islands, Brachyura and Stomatopoda.—*Bulletin of the Raffles Museum* 22: 105–148.
- Van Dover, C. L., R. H. Gore, and P. Castro. 1986. *Echinoecus pentagonus* (A. Milne Edwards, 1879): larval development and systematic position (Crustacea: Brachyura: Xanthoidea nec Parthenopidea).—*Journal of Crustacean Biology* 6: 757–776.
- Ward, M. 1934. Notes on a collection of crabs from Christmas Island, Indian Ocean.—*Bulletin of the Raffles Museum* 9: 5–28.
- Watabe, T. 1974. On spawning seasons of crabs from Sagami Bay.—*Researches on Crustacea* 6: 136–142. [In Japanese.]
- White, A. 1847. Descriptions of new Crustacea from the Eastern Seas.—*Proceedings of the Zoological Society of London* 15: 56–58.
- Wu, P. (editor). 1983. Latin-Chinese marine organism names.—Pp. 1–822. Ocean Press, Beijing, China. [In Chinese.]
- Yamaguchi, T., K. Harada, M. Takeda, and T. Kikuchi. 1987. Crab fauna of the Amakusa Islands.—*Calanus* 10: 1–71.
- Yang, C. M. 1979. A list of Brachyura in the Zoological Reference Collection of the Department of Zoology. Guide no. 14.—Department of Zoology, University of Singapore. Pp. i–viii, 1–60. [Mimeographed.]

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