A R T I C L E

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.

MATERIALS AND METHODS

The abbreviations GI 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 Natuurhistorisch Museum (former Rijksmuseum van Natuurlijke Historie), Leiden, The Netherlands; SMF—Forschungsinstitut Senckenberg, Frankfurt am Main, Germany; USNM—National Museum of Natural History, Smithsonian 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


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 “EU-MÉDON 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 *Eumedon* 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 *Proechinoecus* Ward, 1934, is very apparent. Serène and Romimohtarto (1963: 3) suggested the “... possible inclusion of the two genera *Proechinoecus* and *Echinoecus* in one ...”, although they noted differences between them. In *Proechinoecus*, 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, *Proechinoecus* 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
Eumedon convictor (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 [Hatrang, 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 = Paracel 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 = Paracel 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]; Števčić et al., 1988: 1309 [Philippines, W. Visayas, Philippines, Andaman Sea; Solomon Islands; Line Islands, Pacific Ocean]; Soltanpur-Gargari et al., 1989: 70 [larvae]; Dai and Yang, 1991: 180, fig. 94 [Xisha Islands = Paracel Islands, South China Sea]; Mori et al., 1991: 302 [list only].

Eumedon convicter 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].

Fig. 1. *Echinococcus pentagonus* (A. Milne Edwards, 1879), male, 11.7 x 9.7 mm, Mahe, Seychelles (RMNH 42518): A, dorsal view; B, ventral view.
Reef, reef flat, on *Echinolithix* 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 x 3.7 mm, 5.4 x 4.8 mm, 6.6 x 6.9 mm, and 10.4 x 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. Vandenbiegel, 1988. French Polynesia: 1 ♀ (12.8 x 11.2 mm) (holotype of *Eumedon convexus* Bouvier and Seurat, MNHN MP-B 24733), Hao Island, Tuamotu Archipelago, French Polynesia, collected by V. Noir, 1904; 4 ♀♂ (13.0 x 11.2 mm, 14.0 x 13.0 mm, 11.8 x 10.5 mm, and 13.5 x 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 Ngaruama Island, Raroia Atoll, Tuamotu Islands, collected by J. P. E. Morrison, 2 September 1952. Hawaiian Islands: 2 ♂♂ (SMF TS64), Waikiki, Oahu, on *Echinolithix diadema*, collected by T. Sakai, October 1960; 3 ♂♂, 5 ♀♀ (ZRC 1997.154–161), Oahu, on *Echinolithix calamaris*, collected by P. Castro; 1 ♀ (WAM 92–93), off Eca 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 *Echinolithix calamaris*, Hanauma Bay, Oahu, collected by Hawaii Marine Laboratory; 1 ♂, 1 juvenile ♀ (BPBM 1973.227), from *Echinolithix diadema*, Waikiki, Oahu, 40 feet (12.2 m) depth, collected by Hawaii Marine Laboratory; 1 ♂ (BPBM 1973.227), from *Echinolithix diadema*, Waikiki, Oahu, 40 feet (12.2 m) depth, collected by L. Trott, Hawaii Marine Laboratory; 1 ♂ (BPBM 1973.227), from anal region of *Echinolithix diadema*, off Waikiki, Oahu, 40 feet (12.2 m) depth, collected by L. Trott, Hawaii Marine Laboratory; 1 ♀ (BPBM 1973.227), from *Echinolithix 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 x 16.0 mm) (BPBM 5300) (as *Echinocidus rathbunii*), off Fort D. 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 maxillipeded 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, *Echinolithix 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, *Gonathotus 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 *Eume­denus* 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 *Eumedon 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 margin of the ambulatory leg 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 *Echinoecus 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 [Fig. 2.](#)

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*ECHINOECUS PENTAGONUS* (A. Milne Edwards, 1879), A–I, 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, Manuruzu, 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 zoa to megalopa) was described by Van Dover et al. (1986).

**Host Records.**—Diademata: *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 Okino-shima 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 Kit peninsula, 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)].

**Eumedon 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 *Eumedon pentagonus* A. Milne Edwards, 1879].

**Material Examined.**—Japan: Holotype: δ̅ (6.4 x 6.7 mm) (KMNH 5775), Okino-Shima Island, 34°15’N, 130°06’E, Okinoshima Expedition II, collected 19–29 May 1933; paratypes: 1 φ (allotype) (KMNH 5776), 2 φ (KMNH 5777–8), same data as holotype; 1 juvenile φ (ZRC 1997.151), Kushimoto, on *Acanthocidaris crassispina*, collected by S. Nagai, June 1991, 1 δ (5.1 x 5.5 mm), 2 φ (NSMT), Manazuru, on *Acanthocidaris crassispina*, collected by H. Suzuki, 25 April 1970; 1 δ (4.5 x 4.7 mm), 1 φ (NSMT), Kushimoto, Wakayama Prefecture, associated with *Pseudocentrotus depressus*, collected 4 November 1973; 1 δ (6.2 x 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 anterior rostrum 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, Manuruzu, 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: *Heliocidaris (= Acanthocidaris) crassispina* (Agassiz), and Strongylocentrotidae: *Pseudocentrotus depressus* (Agassiz).

**Distribution.**—Known only from Japan.

**Echinoecus sculptus** (Ward, 1934), new combination

Figs. 41, 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 Romimoiharto, 1963: 2, figs. 1A, 2, pl. 1: figs. A, B [Christmas Island]; Serène, 1968: 63 [list only]; Yang, 1979: 12 [Christmas Island]; Števec et al., 1988: 1312 [list only].

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


**Diagnosis.**—Carapace slightly broader than long, rostrum short; frontal margin trilobed; regions poorly defined; surface of carapace highly pitted and rugose, surfaces of che­lipeds 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* (Linneaus).

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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. *Echinococcus sculptus* (Ward, 1934), new combination, paratype male, 4.7 x 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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