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Crabs from some submarine caves in the Pacific (Crustacea: Decapoda: Brachyura)

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Abstract

Ten species obtained from some submarine caves in the Pacific are recorded: *Dynomene pugnatrix* De Man, 1889 (Dynomenidae), *Hyastenus uncifer* Calman, 1909 (Epialtidae), *Camposcia retusa* (Latreille, 1829) (Inachidae), *Crossotonotus spinipes* (De Man, 1888) (Crossotonotidae), *Carupa tenuipes* Dana, 1852, *Gonioinfradens paucidentata* (A. Milne-Edwards, 1861) and *Laleonectes nipponensis* (Sakai, 1938) (Portunidae), and *Neoliomera cerasinus* Ng, 2002, *N. richtersi* (De Man, 1889) and *Xanthias latifrons* (De Man, 1888) (Xanthidae). Brief comments are presented on three stages of their morphological and ecological adaptation to the dark habitat.

Key words: submarine cave crabs; cavernicolous crabs; cryptic crabs; adaptation to dark habitat

Introduction

The coral reefs in tropical and subtropical waters keep various types of sheltered places for the small invertebrates, and also the submarine caves offer the vast and special habitat to the various kinds of invertebrates and fishes. Some species are specialized morphologically to true dark environments, but the morphological adaptions are not always found in most of the invertebrate species happened to be brought in the caves or with short biological history in the dark habitat. The samplings in the submarine caves are generally difficult for most of the researchers, but recently, the leisure divers attracted to the submarine dark caves rarely brought the unusual species.

Materials and Methods

Under the financial support of the Japanese Government, Dr. T. Kase of the National Museum of Nature and Science, Tokyo, and his team with scientists and professional divers made the researches mainly on the so-called living fossil gastropods not only in the submarine caves of the Ryukyu Islands but also of the oceanic islands scattered in the central and southern Pacific Ocean. The crabs collected as by-products during the field researches entitled “Natural history of submarine cave organisms in Indo-Pacific” were studied by Takeda (1993, 2003, 2010), Ng and Takeda (2003), Takeda and Komatsu (2010), and Komatsu and Takeda (2013), and the contributions based on their submarine cave collections were expanded to the other decapod groups, e.g., hermit crabs by Osawa and Takeda (2004), and caridean shrimps by Brand and Takeda (1994) and Okuno et al. (2003).

Recently, the additional specimens from some Pacific submarine caves kept unrecorded were found in the Tsukuba Research Departments of the National Museum of Nature and Science, Tokyo. The aim of this paper is to record the identification results of these specimens and to leave the information of crab adaptation to dark submarine environments.

Abbreviations used in this paper: NSMT (National Museum of Nature and Science, Tokyo), cb (carapace breadth), cl (carapace length), rl (rostral length), G1 (male first gonopod).

Records of the Species

Family DYNOMENIDAE Ortmann, 1892

Genus *Dynomene* Desmarest, 1823

Dynomene pugnatrix De Man, 1889

(Figs. 1A–E, 2)

Dynomene pugnatrix De Man, 1889, p. 444, pl. 10 fig. 13. —McLay, 1999, pp. 471 (in key), 500, figs. 5d, 11, 22; 2001, p. 810 (in key).

Dynomene pugnatrix brevimana Rathbun, 1911, p. 196.

Material examined

Gustav's Cave (19°19′06.6″N, 155°53′08.4″W), Kona coast, Hawai'i I., Hawaiian Is., 6–8.5 m depth; lava tube, totally dark inside, muddy sand; 1♀ (cb 6.5 mm, cl 6.4 mm), NSMT-Cr 32800; 30-X-1997; collected by Ohashi, Kinjo, Paulay, Kano, Kase.

Remarks

The name of this species has often appeared in the literature (Alcock, 1901, p. 75; Ihle 1913, p. 92; Guinot,

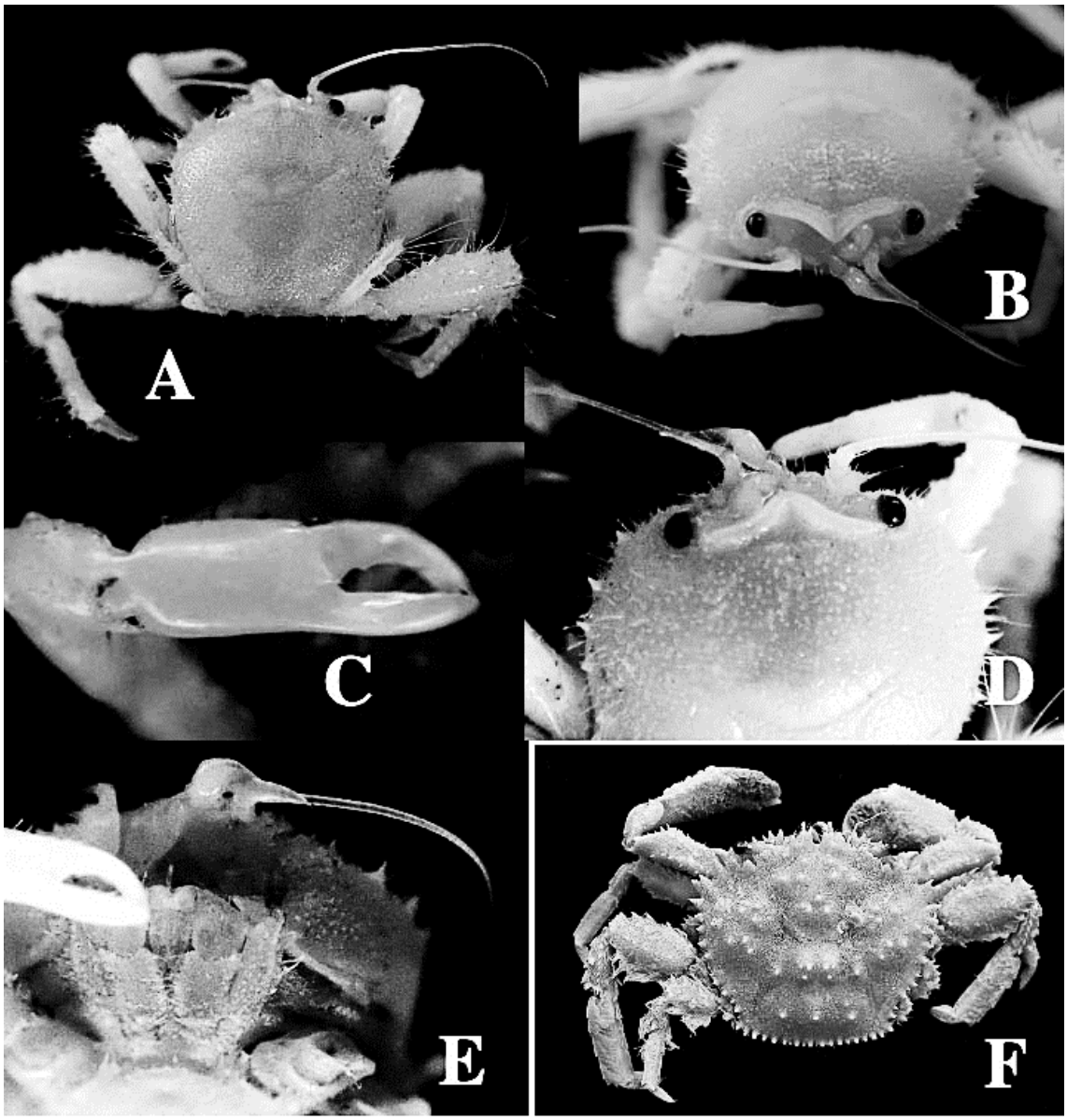

Fig. 1. A–E: *Dynomene pugnatrix* De Man, male (NSMT-Cr 32800; cb 6.5 mm, cl 6.4 mm) from Gustav's Cave, Hawai'i I., Hawaiian Is. Habitus (A). Front-orbital region (B). Right chela (C). Anterior half of carapace (D). Third maxilliped (E). F: *Crossotonotus spinipes* (De Man), male (NSMT-Cr 32803; cb 44.5 mm, cl 37.2 mm) from Goonies Cave, Shimoji-shima I., Rykyu Is.

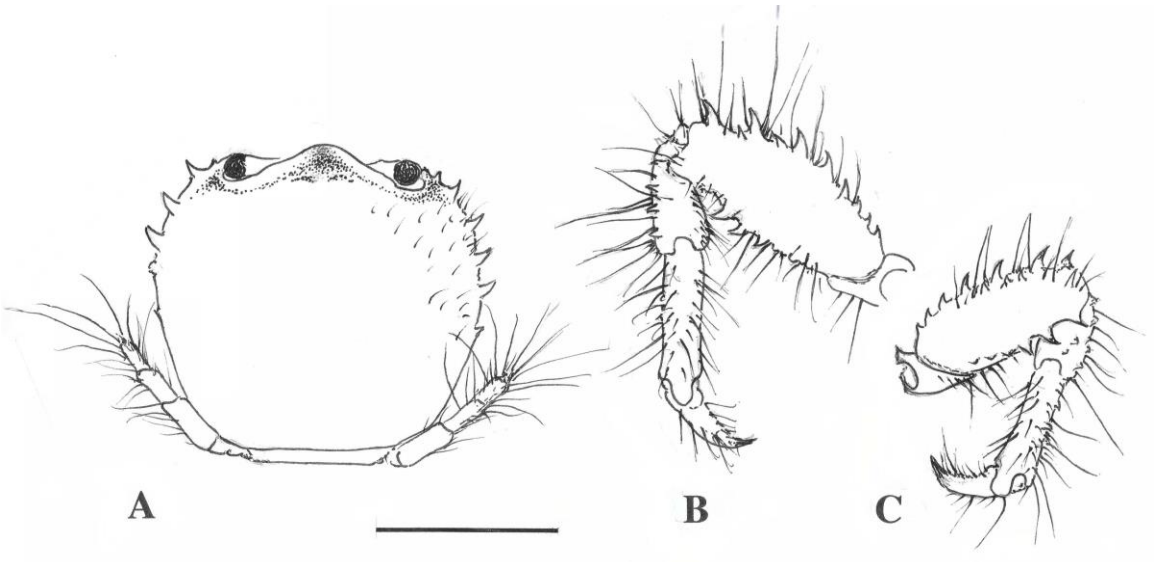

Fig. 2. *Dynomene pugnatrix* De Man, male (NSMT-Cr 32800; cb 6.5 mm, cl 6.4 mm) from Gustav's Cave, Hawai'i I., Hawaiian Is. A: Semi-realistic illustration of carapace, with last pereiopods of both sides. B: Left second ambulatory leg. C: Right third ambulatory leg. Scale = 3 mm.

1967, p. 242; Serène 1968, p. 36; Takeda 1977, p. 35; Ng et al. 2008, p. 37), but the records of the specimens are seen only in De Man (1889, original description) and McLay (1999).

McLay (1999) distinguished four Indo-West Pacific and one Atlantic species in the genus *Dynomene*, and then, two additional species were described by McLay (2001) who prepared the key to all the species including two new species. The present specimen was keyed out to *D. pugnatrix* De Man, 1889, by 1) the carapace anterolateral teeth are well developed and sharply pointed, 2) the carapace tomentum is sparse, with the carapace surface not obscured, and the chelipeds are slender, 3) the carapace anterolateral margin is armed with five teeth, and the anterior margins of the first three pairs of the ambulatory legs are armed with acute tubercles, and 4) the ratio of the carapace breadth to length is less than 1.2, and a pair of lobes behind the frontal margin is not prominent, there is no tuberculated swelling at the subhepatic region, and each dactylus inner margin of the ambulatory legs is armed with five or six spines.

McLay (1999) examined the type specimens of *D. pugnatrix* from Mauritius and its subspecies *D. p. brevimana* Rathbun, 1911 from Providence Island, and considered that both are synonymous simply due to some minor, individual and sexual differences. Both of *Dynamene kroppi* and *D. guamensis* described by McLay (2001) from Guam are, as noted in the original descriptions, generally close to *D. pugnatrix*, but differ in some characters. *Dynamene kroppi* is distinguished from *D. pugnatrix* decidedly by 1) having six, smaller and blunter anterolateral teeth of the carapace (vs. five in *D. pugnatrix*), 2) the ambulatory legs are armed with small and blunt tubercles on the anterior margins (vs. acute tubercles), 3) the long and filiform setae on the carapace (vs. feathered setae), and 4) five or six spines on the inner margins of the ambulatory dactyli (vs. 10 spines). *Dynamene guamensis* is characteristic in 1) having the narrower carapace with less than 1.2 in the ratio of the carapace breadth to length, 2) the presence of a pair of lobes behind the frontal margin and the tuberculated subhepatic swelling, and 3) five or six small spines on inner margin of each ambulatory dactylus.

The present specimen is morphologically closer to *D. pugnatrix* from the western Indian Ocean rather than two species from Guam, *D. kroppi* and *D. guamenis,* both of which are briefly remarked above. Main characters of the present specimen agree well with the

notes and illustrations of the type specimen of *D. pugnatrix* given by McLay (2001): the proportionally narrow carapace is sparsely covered with longish hairs and armed with five strong, equidistance spiniform teeth on each anterolateral margin (Figs. 1A, 2A) (the last two teeth are somewhat damaged in the present specimen); the palm is slender, and the movable finger is curved (Fig. 1C); and the ambulatory legs are strongly armed with sharp teeth (Figs. 1A, 2B–C). This species is otherwise characteristic in having the raised and thickened front-orbital margin (Figs. 1B, D, 2A) and the third maxilliped merus extended and angulated antero-internally (Fig. 1E).

The present specimen shows no morphological speciation for cavernicolous habit and habitat, except for somewhat whitish, semi-transparent color of the carapace, chelipeds and ambulatory legs without special coloration.

Distribution

The type locality is Mauritius, and the other recorded locality is Providence Island, the western Indian Ocean, described as the subspecies. The bathymetric range is 90–140 m (Rathbun 1911, as *D. pugnatrix brevimana*). The present record is remarkable as the fourth of the genus *Dynomene* from the Hawaiian Islands (cf. Castro 2011), being new to the Hawaiian Islands but also to the Pacific.

Family EPIALTIDAE MacLeay, 1838
Genus *Hyastenus* White, 1847
Hyastenus uncifer Calman, 1909
(Fig. 3A–B)

Hyastenus uncifer Calman, 1909, p. 712, pl. 72 figs. 8–9. —Griffin & Tranter, 1986, pp. 125 (in key) and 156, figs. 38e–f, i, 39c, 42e–g. —Marumura & Kosaka, 2003, p. 33, pl. 7 fig. 38. —Poupin et al., 2018, p. 18, fig. 8C. —Ohtsuchi et al., 2020, p. 7, figs. 3D, 6–8.

Material examined

Goonies Cave, Shimoji-shima I., Miyko Group, Ryukyu Is., 1♂ (cb 6.1 mm, cl 9.0 mm in median line excluding posterior tubercle, rl 12.3 mm), NSMT-Cr 32801; 16-XI-1995; collected by local diver.

Remarks

In this species, the carapace is narrowly pyriform (Fig. 3A–B), and the rostral spines are remarkably long, ca. 1.4 times as long as the carapace proper (Fig. 3A). The records in the literature are few, but the fine figures and photographs ready for the species identification were given in the literature cited above. Recently, Ohtsuchi et al. (2020) made the detailed description of and notes on the specimens from the Ryukyu Islands, with the G1 figures.

Distribution

Mayotte Island in the western Indian Ocean, Christmas Island in the eastern Indian Ocean, and the West Pacific (Indonesian waters and the Ryukyu Islands), subtidal to 30 m depth. Inhabitant of coral reef, without special adaptation to dark habitat.

Family INACHIDAE MacLeay, 1838
Genus *Camposcia* Latreille, 1829
Camposcia retusa (Latreille, 1829)
(Fig. 3C)

Material examined

Goonies Cave, Shimoji-shima I., Miyako Group, Ryukyu Is.; 1 young ♀ (cb 5.2 mm, cl 8.2 mm), NSMT-Cr 32802; 18-XI-1995; collected by local diver.

Remarks

This monotypic representative of the genus *Camposcia* is remarkable in having the carapace, chelipeds and ambulatory legs covered thickly with short stiff setae, by which many kinds of invertebrate larvae such as sponges, hydrozoans, bryozoans and ascidians are trapped. The ecological style of such

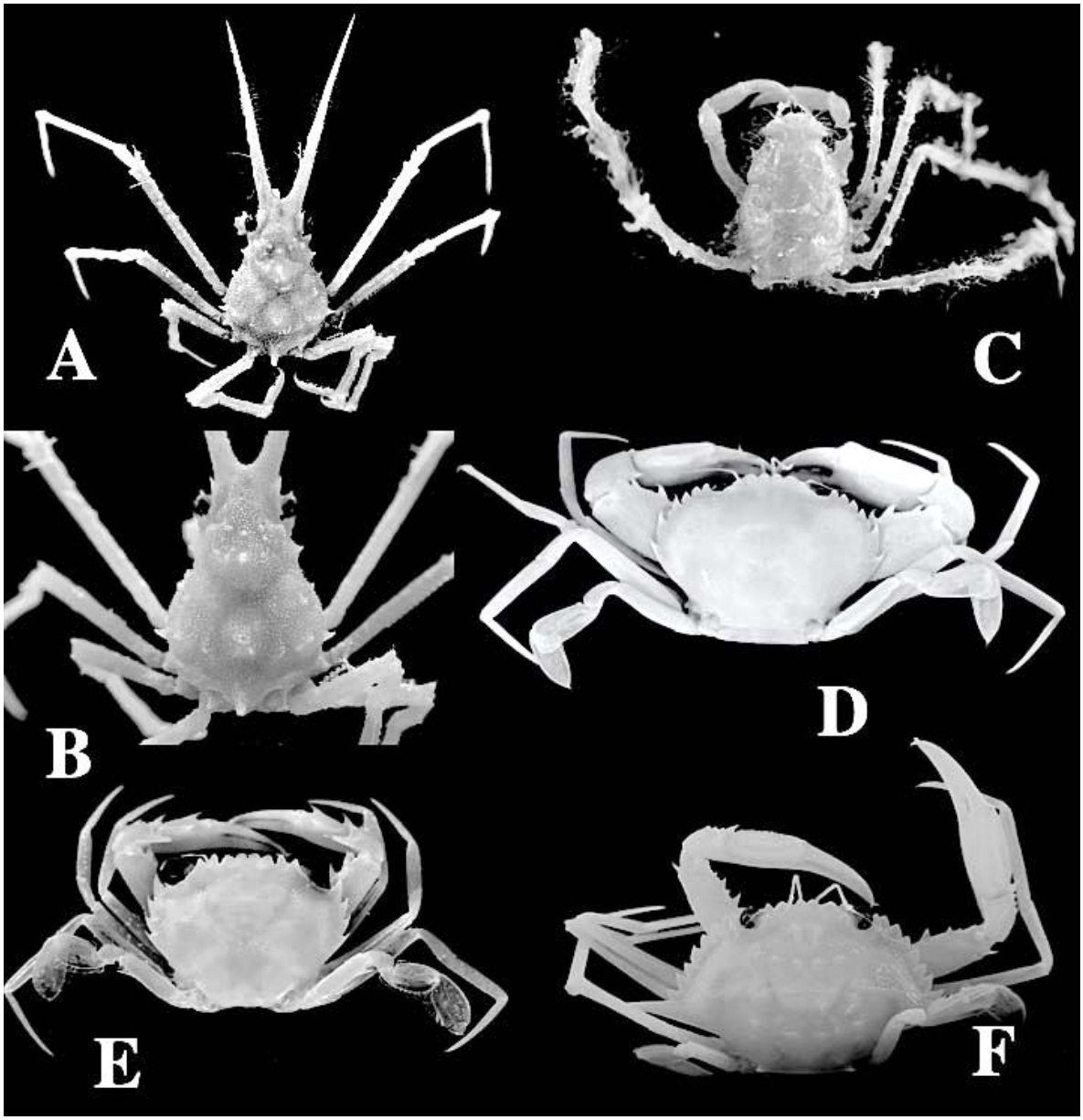

Fig. 3. A–B: *Hyastenus uncifer* Calman, male (NSMT-Cr 32801; cb 6.1 mm, cl 9.0 mm in median line excluding posterior tubercle) from Goonies Cave, Shimoji-shima I., Ryukyu Is. C: *Camposcia retusa* (Latreille), young female (NSMT-Cr 32802; cb 5.2 mm, cl 8.2 mm) from Goonies Cave, Shimoji-shima I. D: *Carupa tenuipes* Dana, male (NSMT-Cr 32804; cb 28.4 mm, cl 18.8 mm) from Maya Cave, Phi Phi Lei Is., Thailand. E: *Gonioinfradens paucidentata* (A. Milne-Edwards), juv. (NSMT-Cr 32806; cb 10.8 mm including lateral teeth of both sides, cl 8.0 mm) from Goonies Cave, Shimoji-shima I. F: *Laleonectes nipponensis* (Sakai), young male (NSMT-Cr 32808; cb 22.9 mm including epibranchial teeth of both sides, cl 13.0 mm) from Gustav's Cave, Hawai'i I., Hawaiian Is.

camouflage is clearly shown in the photographs by Kato and Okuno (2001) and Takeda et al. (2019). This species is otherwise morphologically characteristic in the subtruncated carapace frontal margin and the ambulatory legs becoming longer from the first to the fourth pair (Fig. 3C).

Distribution

Whole Indo-West Pacific, commonly found on coral flat reef and rocky shore, with numerous records in the literature. No previous record of occurrence in submarine cave.

Family CROSSOTONOTIDAE Moosa and Serène, 1981

Genus *Crossotonotus* A. Milne-Edwards, 1873

Crossotonotus spinipes (De Man, 1888)

(Fig. 1F)

Pleurophricus spinipes De Man, 1888 (1887–1888), p. 344, pl. 15 fig. 1.

Menella spinipes: Rathbun, 1906, p. 837, fig. 3, pl. 7 fig. 6. —Edmondson, 1946, (p. 310), fig. 184b; 1962b, p. 12, figs. 2e, 4f. —Sakai, 1939, p. 610, pl. 103 fig. 3.

Manella gardineri Rathbun, 1911, p. 240, pl. 20 fig. 9.

Manella brevimana Ward, 1933, p. 387, pl. 21 figs. 7–8. —Moosa & Serène, 1981, p. 54, figs. 12a–b, 13a.

Crossotonotus spinipes: Sakai, 1965, pp. 187 (in English part) and 81 (in Japanese part), fig. 25, pl. 89, fig. 4; 1976, p. 596 (in English vol.), p. 370 (in Japanese vol.), pl. 206 fig. 1. —Chen, 1975, p. 167, fig. 9, pl. 2 fig. 3. —Dai et al., 1986, p. 414, fig. 229A. —Dai & Yang, 1991, p. 451, fig. 229A. —Castro, 2000, p. 574, figs. 45–46, 51, 61f; 2011, p. 54 (in list). —Castro & Davie, 2003, p. 156. —Kawamoto & Okuno, 2003, p. 150, 1 fig.

Crossotonotus sp.: Takeda & Shimazaki, 1974, p. 75, pl. 2 fig. B.

Material examined

Goonies Cave, Shimoji-shima I., Miyako Group, Ryukyu Is.; 1 ♂ (cb 44.5 mm with lateral teeth, cl 37.2 with frontal teeth), NSMT-Cr 32803; 18-XI-1995; collected by local diver.

Remarks

This species, one of four congeneric species of the genus *Crossotonotus*, is characteristic in its appearance with the flattened carapace dorsal surface displayed with the symmetrically arranged tubercles and fringed with many sharp, marginal teeth, and with the stout chelipeds and ambulatory leg (Fig. 1F). Many photographs were published, but the spinous armature is variable individually and developmentally. Castro (2000) examined numerous specimens from many localities in the whole Indo-West Pacific and decidedly referred *Manella gardineri* Rathbun, 1911 and *M. brevimana* Ward, 1933 to the synonyms of this species.

Distribution

Whole Indo-West Pacific, from reef flat to 146 m depth. The detailed known localities are referred to Castro (2000), without record of occurrence in submarine cave.

Family PORTUNIDAE Rafinesque, 1815

Genus *Carupa* Dana, 1851

Carupa tenuipes Dana, 1852

(Fig. 3D)

Carupa tenuipes Dana, 1852a, p. 85; 1852b, p. 279; 1855, pl. 17 fig. 4. —A. Milne-Edwards, 1861, p. 386. —Klunzinger, 1913, p. 329. —Balss, 1924, p. 5; 1934, p. 505. —Leene, 1938, pp. 10, 145 (in list), 147 (in list); 1940, p. 165, figs. 1–2. —Stephenson & Campbell, 1960, p. 88, pl. 2 fig. 1. —Crosnier, 1962, p. 19, figs. 16–23, pl. 1 fig. 1. —Stephenson & Rees, 1967, p. 5. —Stephenson, 1972a, p. 130; 1972b, p. 28; 1976, p. 12. —Sakai, 1965, pp. 112 (in English part), 47 (in Japanese part), pl. 50 fig. 4; 1976, p. 325 (in English vol.), p. 197 (in Japanese vol.), pl. 110 fig. 3. —Chen, 1975, p. 161, fig. 4. —Yang et al., 1979, p. 78, fig. 2. —Dai & Yang, 1991, p. 199, fig. 106, pl. 24 fig. 3. —Poupin, 1996, p. 29. —Apel & Spiridonov, 1998, p. 172, fig. 4, pl. 1-8 fig. 1. —Minemizu, 2000, p. 229, 1 fig. —Naderloo, 2017, p. 170, figs. 20.1–3. —Newman & Spiridonov, 1999, p. 12. —Koch & Bližňáková, 2023, p. 222, figs, 11, 28.

Carupa laeviuscula Heller, 1862, p. 520; 1865, p. 27, pl. 3 fig. 2. —De Man, 1888 (1887–1888), p. 336; 1902, p. 642. —Alcock, 1899, p. 26. —Borradaile, 1900, p. 578. —Nobili, 1906, p.

189; 1907, p. 386. —Rathbun, 1907, p. 64; 1910, p. 360; 1911, p. 210. —Edmondson, 1925, p. 36; 1946, p. 278 (in discussion), fig. 173a; 1954, p. 226, figs. 3b, 4e–g. —Sakai, 1936 (1935), p. 136, pl. 35 fig. 3; 1939, p. 373, pl. 44 fig. 3. —Ward, 1942, p. 78. —Chen, 1975, p. 162, fig. 5.

Carupa laeviscula [sic]: Leene, 1938, pp. 9, 145 (in list) and 147 (in list).

Carupa tanuipes [sic]: Türkay, 1971, p. 113.

Material examined

Maya Cave (07°40′23.5″N, 98°45′42.7″W), Phi Phi Lei I., Phi Phi Is., Krabi, Thailand, 4.8–9.6 m depth; totally dark to gloomy inside, calcareous mud; 1♂ (cb 28.4 mm, cl 18.8 mm), NSMT-Cr 32804, 1♀ (cb 28.8 mm, cl 19.4 mm), NSMT-Cr 32805; 3-XI-1998; collected by Ohashi, Kinjo, Kase, Hayami.

Remarks

The genus *Carupa* is represented by two species, *C. tenuipes* Dana, 1852 (type species) and *C. ohashii* Takeda, 1993, the differences of which are described in the original description of *C. ohashii*. The color in life is the most characteristic difference in both species, but even in the discolored specimens (Fig. 3D), *C. tenuipes* is readily distinguished from *C. ohashii* with some remarkable differences, viz. the wider and elliptical carapace (vs. the narrower and rather hexagonal carapace in *C. ohashii*), seven more or less lobate anterolateral teeth of the carapace anterolateral margin, with smallest fifth and prominently large sixth teeth (vs. fifth tooth the strongest and much larger than the sixth teeth in *C. ohashii*), the frontal margin with four subequal lobes separated by three subequal notches (vs. median notch much deeper and U-shaped in *C. ohashii*).

Distribution

Widely distributed in the whole Indo-West Pacific, without record of occurrence in submarine caves.

Genus *Gonioinfradens* Leene, 1938

Gonioinfradens paucidentata (A. Milne-Edwards, 1861)

(Fig. 3E)

Goniosoma paucidentatum A. Milne-Edwards, 1861, p. 381, pl. 35 fig. 3.

Thalamita Giardi Nobili, 1905, p. 164.

Charybdis (*Goniosoma*) *Giardi*: Nobili, 1906, p. 115, pl. 5 fig. 23, pl. 7 fig. 34.

Charybdis paucidentata: Rathbun, 1911, p. 206. —Guinot, 1964 (1962), p. 10. —Poupin, 1996a, p. 31; 1996b, p. 34, pl. 16 fig. f. —Takeda, 1998, p. 45, fig. 1B. —Minemizu, 2000, p. 244, 1 fig.

Charybdis giardi (Nobili): Balss, 1924, p. 3.

Charybdis (*Gonioinfradens*) *paucidentata*: Leene, 1938, pp. 24 (in key), 131, figs. 74–76. —Stephensen, 1945, pp. 119, 204 (in table). —Stephenson, 1972b, pp. 10 (in key), 36 (in list). —Sakai, 1976, p. 366 (in English vol.), p. 216 (in Japanese vol.), pl. 130 fig. 1.

Gonioinfradens paucidentata: Apel & Spiridonov, 1998, p. 223, figs. 40–41, pl. 1-8 fig. 7. —Kawamoto & Okuno, 2003, p. 126, 1 fig. —Okuno, 2004, p. 2, fig. 1B. —Naderloo, 2017, p. 187, figs. 20.20–20.22a.

Material examined

Goonies Cave, Shimoji-shima I., Miyako Group, Ryukyu Is.; 1 juv. (cb 10.8 mm including lateral teeth, cl 8.0 mm including frontal teeth), NSMT-Cr 32806; 18-XI-1995; collected by local diver.

HA5 Cavern (19°38′27.6″ S, 174°29.6″W), SW Mo'ong'one I., Ha'apai Group, Tonga, 11–28 m depth; coral sand; 2♂♂ (NSMT-Cr 32807; cb 10.5 mm, cl 8.0 mm; cb 15.8 mm, cl 11.7 mm); XI-1996; collected by Ohashi, Kinjo, Paulay, Hayami, Kase.

Remarks

This species is characterized by the carapace armed with four sharp anterolateral teeth including the

external orbital tooth; each tooth is tipped with a horny spine, and the first two teeth are supplemented each with an accessory spinule at the posterior end (Fig. 3E). The accessory spinules of the first two carapace anterolateral teeth may be variable in size and sometimes almost obsolete, but the armature of the carapace anterolateral teeth is considered to be generic, making this species as monotypic representative distinct from the typical *Charybdis* species.

Distribution

Widely distributed in the Indo-West Pacific, from East Africa and the Red Sea eastwards to the French Polynesia and northwards to Japan in the Pacific. The present specimens were collected in the submarine caves of the Ryukyu Islands and Tonga, and Takeda (1998) recorded this species in the complete dark of the Siaes Cave in the Palau Islands, but this species is sometimes found near entrances or open spaces outside of caves.

Genus *Laleonectes* Manning and Chace, 1990

Laleonectes nipponensis (Sakai, 1938)

(Fig. 3F)

Portunus (*Portunus*) *vacans* (A. Milne-Edwards, 1878) ? : Edmondson, 1935, p. 25, fig. 7.

Neptunus (*Hellenus*) *nipponensis* Sakai, 1938, p. 301, fig. 1, pl. 16 fig. 1; 1939, pp. 386 (in key), 394, figs. 6−7, pl. 82 fig. 1.

Portunus (*Portunus*) *oahuensis* Edmondson, 1954, pp. 236 (in key), 243, fig. 20.

Portunus nipponensis: Stephenson & Campbell, 1959, pp. 89 (in key), 91 (in key). —Serène, 1971, p. 71, figs. A−D. —Stephenson, 1972a, p. 137; 1972b, pp. 14 (in key), 41 (in list). —Crosnier & Thomassin, 1974, p. 1106, fig. 5a–b. —Poupin, 1996a, p. 33; 1996b, p. 36, pl. 17 fig. b.

(Nec) *Portunus nipponensis*: Crosnier & Thomassin, 1974, p. 1106, fig. 5c−d. [= *Laleonectes kuriya* Mendoza & Devi, 2017]

Portunus (*Xiphonectes*) *nipponensis*: Sakai, 1976, pp. 338 (in key), 346 (in English vol.), p. 207 (in Japanese vol.), fig. 186, pl. 119 fig. 3.

Laleonectes nipponensis: Takeda, 1998, p. 45. —Fujita, 2018, p.83 (in discussion), fig. 3E. —Crosnier & Moosa, 2002, pp. 393–395 (in discussion), figs. 3B, 5D–F. —Kawamoto & Okuno, 2003, p. 125, 1 fig. —Poupin et al., 2018, p. 28, fig. 10G. —Mendoza & Devi, 2017, p. 227 (in discussion), figs. 1C–D, 4A–D, 5D–F, 6B–C.

Material examined

Gustav's Cave (19°19′06.6″N, 155°53′08.4″W), W Hawai'i I., Hawaiian Is., 6–8.5 m depth; lava tube, totally dark inside, muddy sand; 1 ♂ (cb 22.9 mm including epibranchial teeth of both sides, cl 13.0 mm), NSMT-Cr 32808; 30-X-1997; collected by Ohashi, Kinjo, Kase, Hayami.

Third Lava Flow Cave (19°15′57.4″N, 155°53′18.9″W), W. Hawai'i I., Hawaiian Is., 4.5–6 m depth; gloomy inside; 2 juvs (cb 14.2 mm, cl 7.6 mm; cb 15.0 mm, cl 7.7 mm); NSMT-Cr 32809; 4-XI-1997; collected by Ohashi, Kinjo, Paulay, Kano, Kase.

Remarks

The general shape of the carapace, chelipeds and ambulatory legs of the present species (Fig. 3F) are just those of the *Portunus* species, but characteristic in having a row of stridulatory granules on each subhepatic region, and the elongated ambulatory legs. The genus *Laleonectes* was established to include *Neptunus vocans* A. Milne-Edwards, 1878 from the eastern Atlantic and *N.* (*Hellenus*) *nipponensis* Sakai, 1938 from the Indo-West Pacific based on the presence of stridulatory granules. Later, two new species, *L. stridens* Crosnier and Moosa, 2002 and *L. kuriya* Mendoza and Devi, 2017, were described as the third and fourth in the genus and the third for the Indo-West Pacific.

Distribution

Whole Indo-West Pacific, being often found in the submarine caves.

Family XANTHIDAE MacLeay, 1838
Genus *Neoliomera* Odhner ,1925
Neoliomera cerasinus Ng, 2002
(Figs. 4, 5A–C)

Neoliomera cerasinus Ng, 2002, p. 95, figs. 1−5.
—Kawamoto & Okuno, 2003, p. 137, 1 fig.
—Fujita et al., 2013, p. 5, figs. 4–5.

Material examined

Worm Cave (20°35′21.6″ N, 156° 25′49.2″ W), SW Maui I., Hawaiian Is., 22−32 m depth; lava tube, totally dark, muddy sand; 1♂ (cb 30.0 mm, cl 18.0 mm), NSMT-Cr 32810; 21-X-1997, Ohashi, Kinjyo, Paulay, Kano, Kase leg.

Marigondon Cave (10°15.8′ N, 123° 59.2″ E), Mactan I., Philippines, 25 m depth; 1♂ (cb 30.7 mm, cl 19.1 mm), NSMT-Cr 32811, 1♀ (cb 22.3 mm, cl 14.1 mm), NSMT-Cr 32812; 25–27-XI-1998; M. Takeda leg.

Hidenchi-gama Cave, Kume-jima I., Ryukyu Is., 38 m depth; 1 carapace (cb 30.5 mm, 19.0 mm), 1 juv. (cb 15.1 mm, cl 9.6 mm), NSMT-Cr 32813; 9-IX-1999; collected by local diver. The right branchial part of this juvenile is somewhat deformed probably with isopod parasite in the gill chamber.

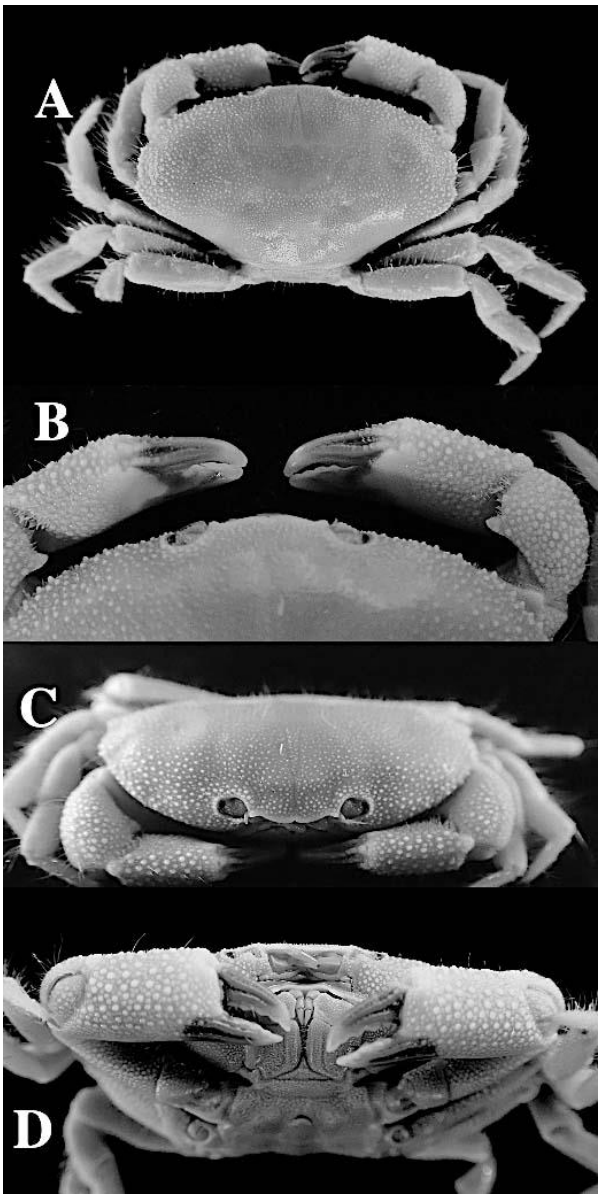

Fig. 4. *Neoliomera cerasinus* Ng, male (NSMT-Cr 32810; cb 30.0 mm, cl 18.0 mm) from Worm Cave, Maui I., Hawaiian Is. A: Habitus. B, C: Anterior part of carapace, dorsal and frontal views. D: Both chelipeds.

Remarks

This species was elaborately described and finely figured by Ng (2002) based on the specimens from underwater caves in Christmas Island and the Ryukyu Islands. The present specimens agree generally with the original description in the shape of the carapace and chelipeds, with minor variation of the carapace anterolateral margins. The carapace (Figs. 4A, 5A) is transversely oval, covered sparsely with minute granules on the most part of dorsal surface and with slightly larger granules along the lateral margins, and poorly divided into regions only with furrows dividing the frontal and gastric regions. The carapace anterolateral margin (Fig. 4A) is entire for its anterior two-thirds, with a fringe of small granules, and divided into two parts for its posterior one-third, with two shallow depressions. This typical formation of the carapace anterolateral margin is seen in Fig. 4A, but the anterior depression of the two is sometimes so shallow and indistinct that the posteriormost part is

only distinguished in the photographs. In the present specimens from Marigondon Cave in the Philippines, the carapace anterolateral margin is armed with almost equidistant larger granules, with the indistinct depressions (Fig. 5A).

The length of the chelipeds and also the curvature of the movable fingers may be referred to the size or sex differences. In both specimens of similar size from Hawaii and Philippines, the movable finger is strongly curved and leaves a space between the immovable finger in the male from Philippines (Fig. 5B–C) somewhat like the chela of the holotype, but almost straight without space in the male from Hawaii (Fig. 4D). In the Philippine specimen, the fingers are sculptured with deep longitudinal furrows on each surface (Fig. 4B, D), and may change drastically to the curved fingers at the next ecdysis. The G1 is quite similar to the figures of the holotype G1 given by the original author (Ng 2002: fig. 5), having about 15 long plumose hairs at the distal part.

Distribution

Originally reported from the submarine caves in Christmas Island in the Indian Ocean, 5-10 m depth, and Kume-jima Island in the Ryukyu Islands, 35 m depth. Then, it was recorded also from submarine caves in Kume-jima Island by Kawamoto and Okuno (2003), and off Shimoji-shima Island in the Ryukyu Islands, 16–23 m depth (Fujita et al. 2013).

Neoliomera richtersi (De Man, 1889)
(Fig. 5D)

Actaeodes richtersii De Man, 1889, p. 412, pl. 9 fig. 2.
Actaeodes Richtersii: De Man, 1890, p. 51.
Liomera richtersi: Ortmann, 1894, p. 451. —Borradaile, 1900, p. 583.
Liomera Richtersi: Nobili, 1907, p. 387.
Neoliomera richtersi: Odhner, 1925, p. 33, pl. 2 fig. 13. —Forest & Guinot, 1961, p. 79, fig. 74. —Edmondson, 1962a, p. 252, fig. 9e. —Sakai, 1969, p. 265 (in discussion), fig. 10. —Castro, 2011, p. 100 (in list).
(Nec) *Neoliomera richtersi*: Sakai, 1967, pp. 72 (in Japanese), 81 (in English), frontispiece fig. 1. [= *N. richteroides* Sakai, 1969]

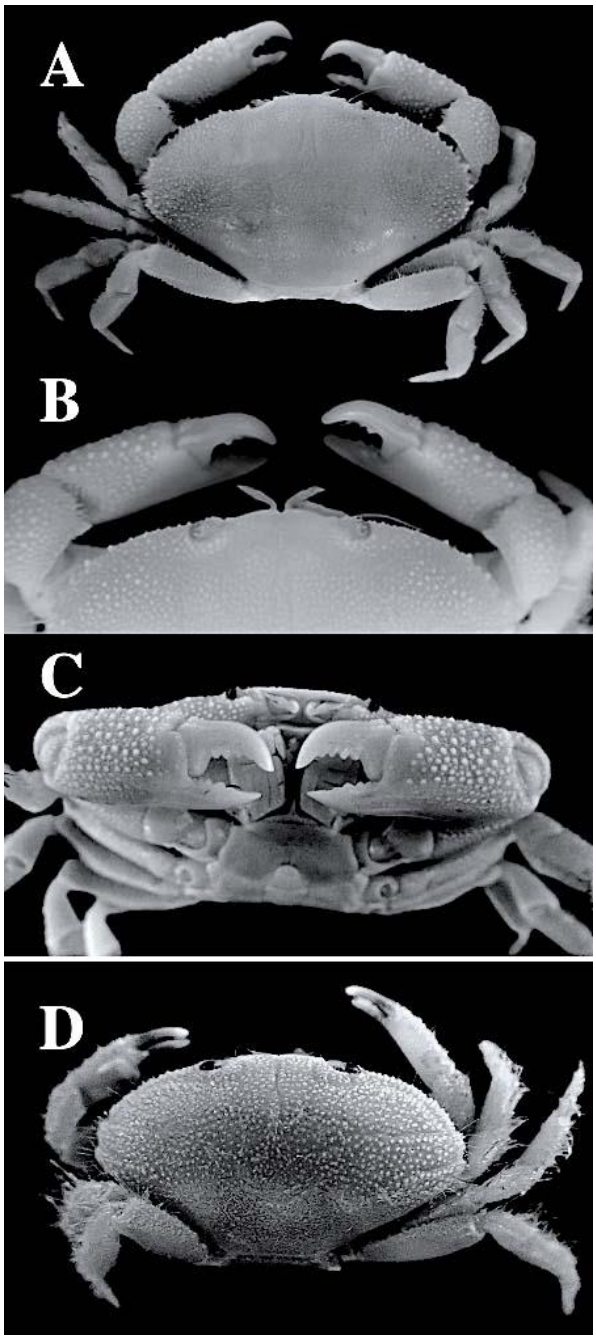

Fig. 5. A–C: *Neoliomera cerasinus* Ng, male (NSMT-Cr 32811; cb 30.7 mm, cl 19.1 mm) from Marigondon Cave, Mactan I., Philippines. Habitus (A) and both chelae (B, C). D: *Neoliomera richtersi* (De Man), male (NSMT-Cr 32814; cb 16.3 mm, cl 9.1 mm) from Third Lava Flow Cave, Hawai‘i I., Hawaiian Is.

Material examined

Third Lava Flow Cave (19°15′57.4″N, 155°53′18.9″W), W. Hawai‘i I., Hawaiian Is., 4.5–6 m depth; gloomy; 1♂ (cb 16.3 mm, cl 9.1 mm), NSMT-Cr 32814, 1 juv. (cb 6.5 mm, cl 3.8 mm), NSMT-Cr 32815; 4-XI-1997; collected by Ohashi, Kinjo, Paulay, Kano, Kase.

Remarks

In the male examined (Fig. 5D), the carapace is transversely oval, with 1.8 in the ratio of cb and cl, being covered thickly with pearly granules and rather sparsely with silky hairs; the dorsal areolation is shown by the longitudinal shallow furrows separating the gastric regions; the marginal furrow along the supraorbital margin is distinct and extends to the posterior end of the carapace anterolateral margin, making the thick margin fringed with a line of sharp granules. The carapace anterolateral margin is entire and regularly convex for its anterior two-thirds, and two irregular interruptions along the posterior one-third; two shallow, transverse furrows from the two interruptions. In the present male, with cb 16.3 mm, the chelipeds are slender, and the dark color of the immovable finger extends onto the basal one-fourth of the palm outer surface. Another specimen is much smaller and still juvenile, but the general shape, granulation and hairiness are quite similar to the adult specimen except for the sharper carapace anterolateral margin.

The G1 has several long, simple hairs at the distal part, and is quite similar to the fine figure given by Forest and Guinot (1961: fig. 74).

Distribution

Known only from the Pacific Ocean; New Guinea (Odhner 1925), Palau (Odhner 1925), Rotuma (Borradaile 1900), Marutea (Nobili 1907), Ellice (Odhner 1925), Tuamotu and Tahiti (De Man, 1889, 1890; Ortmann 1894; Odhner 1925; Forest and Guinot 1961), and Hawaii (Edmondson 1962a).

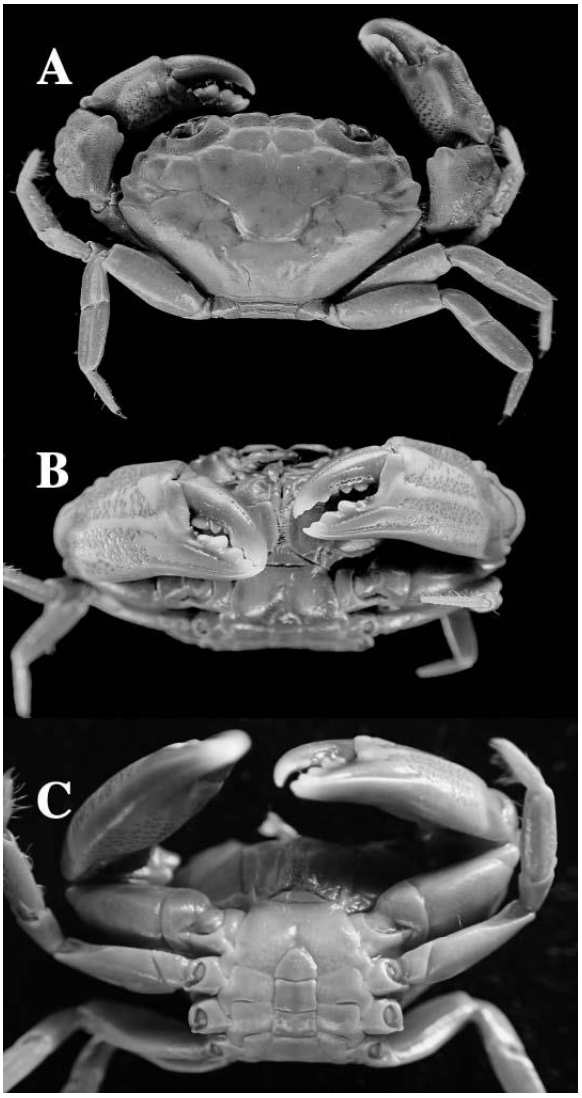

Fig. 6. *Xanthias latifrons* (De Man), male (NSMT-Cr 32816; cb 18.5 mm, cl 12.0 mm) from Third Lava Flow Cave, Hawai‘i I., Hawaiian Is. Habitus, dorsal (A) and ventral (C) views. Chelae (B). Grayish parts of inner and outer surfaces of both palms (Figs. A–B) were blackish in life.

Genus *Xanthias* Rathnun, 1897

Xanthias latifrons (De Man, 1888)

(Fig. 6)

Panopeus latifrons De Man, 1888 (1887–1888), p. 265, pl. 9 fig. 4.

Xanthodes minutus Rathbun, 1893, p. 238.

Xanthias minutus (Rathbun, 1893) : Rathbun, 1906, p. 855, pl. 9 fig. 14; 1911, p. 225.

Chlorodius tuberosicarpus Klunzinger, 1913, p. 230, pl. 1 fig. 9, pl. 6 fig. 12.

Xanthias latifrons: Sakai, 1939, pp. 466 (in key), 468, fig. 32; 1976, pp. 427 (in key), 429 (in English vol.), p. 255 (in Japanese vol.), pl. 155 fig. 1.—Edmondson, 1962a, pp. 242 (in key), 244, figs. 4f, 7e. —Forest & Guinot, 1961, p. 70, fig. 67. —Takeda, 1976, p. 94, pl. 10 fig. D. —Sèrene, 1984, p. 193 (in key), 194 (in key), 198, fig. 117, pl. 28 fig. B. —Monteforte, 1987, p. 9 (in table 1). —Poupin et al., 1996a, p. 50 (in list). —Neumann & Piridonov, 1999, p. 40.

Material examined

Third Lava Flow Cave (19°15′57.4″N, 155°53′18.9″W), W. Hawai'i I., Hawaiian Is., 4.5–6 m depth; gloomy; 2♂♂ (cb 18.5 mm, cl 12.0 mm, NSMT-Cr 33816; cb 10.4 mm, cl 7.0 mm, NSMT-Cr 32817); 4-XI-1997; Ohashi, Kinjo, Paulay, Kano, Kase leg.

Remarks

This species has been referred to some genera, but at present is known as one of 14 reliable *Xanthias* species from the Indo-West Pacific (Ng et al. 2008; Mendoza 2013, 2014). In the present specimen (Fig. 6), the carapace dorsal surface is smooth and distinctly divided into regions by narrow and deep furrows; the frontal and epigastric regions are prominent and similar in size; the epigastric region is separated from the protogastric region, and its outer end reaches to the median part of the protogastric anterior margin; the protogastric region is the biggest among the dorsal regions, and nearly entire, only with a short faint incision from the median part of the anterior margin. The carapace anterolateral margin is armed with four stout, obtuse teeth directed obliquely forward; the first tooth is completely confluent with the external orbital angle and really forms the external orbital angle itself. The chelipeds are comparatively heavy, and slightly different in size; the outer surface of the carpus is divided into several nodules, and the inner angle is armed with two lobate or nodular teeth arranged above and below; in the larger male (cb 18.5 mm), the inner and outer surfaces of the palm are mostly covered with brownish color which may be blackish in life, but in the smaller male (cb 10.4 nmm), the dark-color is extended onto the distal half of the palm in the larger cheliped, but restricted to the basal part of the immovable finger.

The general formation of the carapace and chelipeds of this species is close to that of *X. dawsoni* Takeda and Webber, 2006 from Raoul Island in the Kermadec Islands. Takeda and Webber (2006) correctly compared the new species with *X. glabra* Edmondson, 1951, but it is noted at present that *X. dawsoni* is also close to *X. latifrons*. However, *X. dawsoni* differs from *X. latifrons* by the features that the protogastric region is completely subdivided into two, and the first anterolateral tooth is distinctly isolated from the external orbital angle. It should be pointed at present that some of the paratype specimens may belong to *X. latifrons*, not to *X. dawsoni*, due to the imperfect subdivision of the protogastric region and the fusion of the first anterolateral tooth with the external orbital angle, which were considered by the original authors as the developmental variations.

Distribution

This species is known by rather few records, but widely distributed from the western Indian Ocean and the Red Sea to Tahiti, Hawaii and Japan in the Pacific, from coral reef to the depths of 65 m.

Discussion

Osawa and Fujita (2019) recorded 14 species of submarine cave hermit crabs from the Ryukyu Islands and distinguished three categories of adaptation to the submarine cave habitat. They are the species which 1) prefer silty or sandy substrate in completely dark environment, 2) do not live in complete darkness, but prefer silty or sandy substrate environment, and 3) usually live in cryptic habitats of coral or rocky reefs and opportunistic in submarine caves. The hermit crab habit and habitat may be restricted in various ways by

the dwelling shells and therefore somewhat different from the free-living crabs.

Most of the cavernicolous crabs studied by the present author are not always morphologically specialized, but there may be some stages in relation with their habit and habitat, and partly comparable with the categories of the submarine cave hermit crabs studied by Osawa and Fujita (2019). In the present paper, the distinguished stages for the crabs are, (1) *Species without special adaptation to cave habitat* —The species unexpectedly carried into the caves without morphological modification, including the species associated with some invertebrates such as corals and sponges rather than the cave habitat; (2) *Species using caves as protected habitat* —The species using the caves to protect themselves from predators; (3) *Species completely adapted to cave habitat* —The species completely adapted to the cave dark habitat and morphologically specialized.

The evaluation of adaptation to the submarine cave habitat based only on the morphology of the carapace, chelipeds and ambulatory legs may be not always accurate, but the brief notes on the submarine cave crabs dealt with by the present author and some Japanese researchers are provided in the following lines alongside the three categories.

1) Species without morphological adaptation to cave habitat

Considering the records in the literature up to now without special comments on the habit and habitat, the occurrence of *Hyastenus uncifer* Calman, 1909 (Epialtidae, Fig. 3A–B), *Camposcia retusa* (Latreille, 1829) (Inachidae, Fig. 3C) and *Xanthias latifrons* (De Man, 1888) (Xanthidae, Fig. 6) in dark submarine caves recorded in this paper are, without doubt, casual, although it is not sure when the larvae or juveniles or adults came into the caves. Three of five species from the submarine caves around the Miyako Islands Group (Fujita, 2018), *Dromia dormia* (Linnaeus, 1763) which is now the type and monotypic representative of the genus *Tumidodromia* McLay, 2009 (Dromiidae), *Carpilius convexus* (Forskål, 1775) (Carpilidae) and *Schizophrys aspera* (H. Milne Edwards, 1834) (Majidae) are considered to be casual occurrence. *Schizophrys dahlak* Griffin and Tranter, 1986 (Majidae) recorded by Takeda (1988) from the cave in the Palau Islands is also referred to the unusual occurrence. Most of the so-called spider-crabs including *S. dahlak* are usually cryptic and covered with dust, small pieces of seaweed and various kinds of invertebrates, without the reduced eyestalk and cornea.

Gaillardiellus holthuisi Takeda and Komatsu, 2010 (Xanthidae), from the Marigondon Cave, Mactan Island, the Philippines, was considered to be nearly identical with *G. bathus* Davie, 1997, by Maenosono (2021), although the teeth of the male fingers are rather abnormally developed. Takeda and Komatsu (2010) mentioned that *G. holthuisi* is not an obligate species of the cave fauna because of no special metamorphosis. Its deformed chelae may be one of the sexual characters, not the results of adaption to the cave habitat.

Naruse and Fujita (2015) discovered a new species of the family Xanthidae, *Lipkemera iejima*, in the submarine cave at Ie-jima Island, Ryukyu Islands. The specimens were said to be collected from holes on walls of the cave. The species is the fifth representative of the genus, and generally close to the genus *Liomera* species, in which the carapace is convex, transverse and seemingly heavy against the narrow ambulatory legs. *Lipkemera iejima* seems to be not always cavernicolous in its ecology.

Merratha angusta (Rathbun, 1906) (Xanthidae) and *Paraxanthus pachydatylus* (A. Milne-Edwards, 1867) (Xanthidae) and *Pilumnus cursor* A. Milne-Edwards, 1873 (Pilumnidae) recorded by Takeda and Okuno (2020) from the Nakaccho Cave in Hachijo-jima Island are considered, without doubt, to be settled by chance in a small cave without special adaptative characters.

Lentilumnus latimanus (Gordon, 1934) (Pilumnidae) reported from the submarine caves in the Palau Islands by Takeda (1998) who reported numerous specimens of *L. latimanus* obtained from aquiferous system of unidentified demosponges and calcareous sponges in caves. As the association with sponges has not been mentioned by Gordon (1934, original description, as *Glabropilumnus*) and Garth and Kim (1983, as *Glabropilumnus*), but these small characteristic crabs are considered to be strongly associated with sponges rather than dark caves. Komatsu and Takeda (2013) recorded *Luciades agana* Kropp and Manning, 1996 (Cryptochiridae) from submarine cave in Tonga. This species is one of the smallest not only in the cryptochirid crabs but in the crabs as a whole, being originally described from Guam as a symbiont of screlactinid coral. The Tonga specimen was picked up from substrate brushed out from the wall of the cave, but there is no doubt that the species is a symbiont of coral and not true cavernicolous in habitat. In these two species, the dispersal of the larvae and the settlement to the hosts in the field will be possible only by chance with changeable water current and wave. They are not always morphologically distinctive from the related species in each family, and therefore, may be referred to the same species group as in this first category.

2) Species using caves as protected habitat

Carupa ohashii Takeda, 1993 (Portunidae) was originally reported from some submarine caves in the Ryukyu Islands as the second species of the genus *Carupa* Dana, 1851. Another *Carupa* species, *C. tenuipes* Dana, 1852, is also often found in the caves, as recorded in this paper (Fig. 3D), but both species are found also in the crevice or interstices of coral reefs or at the open space to cave entrance (Fujita, 2018). Their relatively long ambulatory legs are indicative of the adaptive possibility to the cave habitat, but the other morphological characters are not specially adapted to the dark habit and habitat. Such the varied habitat may be made possible by the strong swimming ability peculiar to portunid crabs of certain size.

Two portunid crabs having the long ambulatory legs, *Gonioinfradens paucidentata* (A. Milne-Edwards, 1873) recorded by Takeda (1988; Fig. 3E in the present paper) and Okuno (2004), and *Laleonectes nipponensis* (Sakai, 1938) recorded by Takeda (1998; Fig. 3F in the present paper) and mentioned by Fujita (2018) are widely distributed in the Indo-West Pacific and also often found in the submarine caves. *Laleonectes nipponensis* has a line of stridulatory granules at the sub-hepatic to sub-branchial regions, but it is unknown whether their special organ is used or not for communication in dark caves.

Takeda (2010) described a new crab of the family Portunidae, *Catoptrus marigondonensis* from the Marigondon Cave, and Fujita and Naruse (2011) described the closely related *C. iejima* from submarine cave at Ie-jima Island, southern Ryukyu Islands. Both species are small, having the depressed carapace, and seem to be not good at swimming. Afterwards, Naruse and Uyeno (2021) described *C. lavicolus* from shallow subtidal lava rock field at Sakurajima, an active volcano in Kagoshima Bay, Kyushu, southern Japan. The specimens were said to be collected from deep inside of large lava rocks, with ecologically similar to the submarine caves found in the two congeneric species, *C. marigondonensis* and *C. iejima*. They are all pinkish or brick-red in color, but more or less translucent as a whole, indicating the advanced adaptation to the dark habitat rather than the larger swimming crabs mentioned above.

Fujita et al. (2013) recorded *Neoliomera cerasinus* Ng, 2002 (Xanthidae) from submarine caves off Shimoji-shima Island, Miyako Islands Group, southern Ryukyu Islands. In this paper, *N. cerasinus* was obtained from the submarine caves of the Ryukyu Islands, the Philippines and the Hawaiian Islands (Figs. 4, 5A–C), and also *N. richtersi* (De Man, 1889) from the Hawaiian Islands (Fig. 5D). The genus *Neoliomera* is represented by 17 species (Ng et al. 2008; Mendoza

2023) which are often found in the caves, with reddish color as in *N. insularis* (Adams and White, 1849) and *N. intermedia* Odhner, 1925 (Sakai 1976, pl. 141 fig. 2, pl. 142 fig. 3; Minemizu 2000, 3 figs.), brick red as in *N. cerasinus* Ng, 2002 (Kawamoto and Okuno 2003, 1 fig.; Fujita et al. 2013, fig. 4), reddish or yellowish with white blotches as in *N. richteroides* Sakai, 1969 (Sakai 1967, frontispiece fig. 1, as *N. richtersi*; 1976, pl. 142 fig. 2), *N. demani* Forest and Guinot, 1961 (Sakai 1967, frontispiece fig. 2; 1976, pl. 142 fig. 1, as *N. pubescens* (H. Milne Edwards)), and *N. richteroides* Sakai, 1969 (Sakai 1976, pl. 142 fig. 2), bright red to crimson with regularly arranged white spots as in *N. fragraea* Ho and Ng, 2014 (Ho and Ng 2014, fig. 1), brick red with about 20 reddish spots as in *N. moana* Poupin and Starmer, 2013 (Poupin and Starmer 2013, fig. 1), and solid deep red or purplish red in *N. sabaea* (Nobili, 1906) and *N. foresti* (Serène, 1984) (Mendoza 2023, fig. 19A–C). There seems to be no special morphological modification to the dark habitat, but the color may melt into the cave darkness. The general color patterns of the *Neoliomera* species mentioned above may contribute to protect themselves from the predators, but the movement ability seems to be much lower than the portunid crabs.

Many crab species are cryptic in general, and the underwater large-scale caves for the submarine crabs may be ecologically equivalent with the interstices of coral rubble or subtidal rocks for the cavity dwellers in coral reefs and rocky shore. *Conleyus defodio* P. K. L. Ng and N. K. Ng, 2003 (Goneplacidae) described as a new genus and a new species from deep rubble beds in Guam may be the typical case, with the flattened carapace dorsal surface, the long and slender ambulatory legs, the reduced pigmentation and the small eyes.

3) Species completely adapted to cave habitat

Two new cavernicolous swimming crabs belonging to a new genus *Atoportunus* described by Ng and Takeda (2003), viz. *A. gustavi* from Guam, the Ryukyu Islands, and Christmas Island in the Indian Ocean, and *A. pluto* from Hawaii. Their remarkably long and slender chelipeds and ambulatory legs and also the specialized fingers with some long spines instead of teeth along the grasping margins of both fingers are persuasive for the adaption. Takeda (2003) reported another congeneric species, *A. dolichopus* from the submarine cave at Kume-jima Island, southern Ryukyu Islands. This species is morphologically different from the two known species, but basically same construction as for the carapace, chelipeds and ambulatory legs. However, the chelipeds and ambulatory legs are longer and slenderer, and seem to be pronouncedly adapted for moving and catching the few small animals in the true dark. However, the eyes are not reduced at all unlike some freshwater cave crabs such as *Cerberusa caeca* Holthuis, 1979 (Potamidae) from Borneo, and *Sundathelphusa cavernicola* (Takeda, 1983) (Parathelphusidae) from the Philippines, and the deepwater hydrothermal vent crab of the family Bythograeidae such as *Gandalfus yunohana* (Takeda, Hashimoto and Ohta, 2000) from off the Pacific coast of Japan.

Recently, a remarkably specialized crab of the family Plagusiidae, *Caligoplagusia okinawa*, was described by Fujita and Naruse (2024) based on a pair of specimens from semi-submerged marine cave on the limestone shore of Okinawa-jima Island, the Ryukyu Islands, at depth of 1 m. The habitat is different from the deeper submarine cave, and also the species apparently belongs to the shore crab group, but its specialized shape of the carapace, chelipeds and ambulatory legs brings the *Atoportunus* species of the family Portunidae to mind. Another species perfectly adapted to underwater dark habitat, *Christmaplax mirabilis* Naruse and Ng, 2014, should be mentioned, although the species is an inhabitant of Chiristmas Island in the eastern Indian Ocean, Australia.

The specimens were described as the representative of a new family (Christmaplacidae), a new genus (*Christomaplax*) and a new species (*C. mirabilis*),

having cavernicolous adaptations such as the reduced eyes, the elongated ambulatory legs and pale color. The morphological image of this peculiar crab is similar to that of *C. okinawa* of the Plagusiidae mentioned above rather than that of the anchialine *Orcovita* species of the Varunidae.

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