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Systematics and Zoogeography of Eastern Pacific Stenopodidean Shrimps (Crustacea: Decapoda)

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ABSTRACT.—There are few records of stenopodidean shrimps from the eastern Pacific. Recent research has revealed at least five species in this area. The Stenopodidea is an infraorder of mainly tropical decapods divisible into two distinct ecological groups: (1) a shallow-water coralline habitat group (*Odontozona rubra*, *Microprosthema emmiltum*, and *Stenopus hispidus* in the eastern Pacific) and (2) a group mostly commensal in deep-water hexactinellid sponges (*Spongicoloides galapagensis* and *Odontozona spongicola* in the eastern Pacific). Stenopodidean shrimps of the genera *Stenopus* and possibly *Odontozona* have larval stages with the capacity for long-distance dispersal, so there is a strong probability that other stenopodids are present in the coralline habitats of the eastern Pacific. *Microprosthema emmiltum* is a geminate species of the western Atlantic *Microprosthema semilaeve*. The number of recognized species of stenopodidean shrimps in the eastern Pacific is low mainly because of the cryptic behavior of the shallow-water coralline species and lack of sampling for the deep-water commensals of hexactinellid sponges. Further study both shallow water and deep water in the eastern Pacific will probably yield new species and produce range extensions for known species of stenopodids. Illustrations, diagnoses, and a key to the five recognized eastern Pacific species of stenopodids are presented.

RESUMEN.—La información disponible acerca de 108 camarones stenopodideos del Pacifico es escasa. Estudios recientes acerca de estos organismos han revelado la presencia de por lo menos 5 especies en esta área geográfica. Los Stenopodidea forman una infraorden de decápodos, principalmente tropicales, que pueden ser divididos en dos grupos ecológicos distintos: (1) un grupo que encuentra su habitat en corales de aguas someras (*Odontozona rubra*, *microprosthema emmiltum* y *Stenopus hispidus* en el Pacífico este) y (2) un grupo que es principalmente comensal de las esponjas Hexactinellida de aguas profundas (*Spongicoloides galapagensis* y *Odontozona spongicola* en el Pacífico este). Los camarones stenopodideos del género *Stenopus*, y posiblemente del género *Odontozona*, poseen estadios larvarios con capacidad para dispersarse sobre distancias muy largas, de tal manera que existe una gran probabilidad que otras especies de stenopodideos se encuentren presentes en el habitat coralino del Pacífico este. *Microprosthema emmiltum* es una especie gemela de *Microprosthema semilaeve* que se encuentra en el Atlántico oeste. El bajo número de camarones stenopodideos reconocidos en el Pacífico se debe principalmente al comportamiento críptico de las especies que ocupan las zonas coralinas someras y a la ausencia de muestreos para recolectar los comensales de las esponjas Hexactinellida de aguas profundas. Estudios complementarios en el Pacífico este, tanto en aguas someras como en aguas profundas, probablemente permitirán descubrir especies nuevas y ampliar los límites de distribuciones de las especies de stenopodideos conocidas. Se presentan ilustraciones, diagnosis y una clave de identificación de las 5 especies de stenopodideos conocidas del Pacífico este.

INTRODUCTION

Five stenopodidean shrimps are known from the eastern Pacific. The first reported specimen was collected by the U.S. Fish Commission Steamer "Albatross" in 1888. Ninety-two years later, it was described as a new species, *Spongicoloides galapagensis* Goy, 1980. Subsequent collections by Th. Mortensen in 1916 at Taboga Island, Panama, yielded two more species, *Microprosthema emmiltum* Goy, 1987, and *Stenopus hispidus* (Olivier, 1811). Additional specimens of *M. emmiltum* were collected by W. Schmitt in 1933 and 1934 from the Galapagos Islands and by A. Kerstitch in 1981, 1989, and 1990 from the Gulf of California. The fourth stenopodid found in the eastern Pacific is *Odontozona rubra* Wicksten, 1982, based on material collected in 1979 and 1981 in Mexico, but a specimen that remained unidentified in the Allan Hancock Collection was collected earlier in 1935 from Gorgona Island, Colombia. *Odontozona spongicola* (Alcock and Anderson, 1899) was originally described from two specimens found in the Indian Ocean and was the last stenopodidean shrimp collected from the eastern Pacific in, 1950 by the R/V "Velero IV" off Santa Catalina Island, California. The present paper reviews the records of these five species in the eastern Pacific, their systematics, and zoogeography. It also discusses other stenopodidean shrimps that are likely to be found in this region with more extensive sampling of shallow and deep water.

MATERIALS AND METHODS

Specimens utilized in this study were made available from the museum collections under the care of Drs. A. Bruce, J. Haig, R. Manning, and T. Wolff. Additional uncatalogued specimens of *Microprosthema emmiltum* were supplied by Mr. Alex Kerstitch

(Sea of Cortez Enterprises, Tucson, Arizona). Abbreviations used in the text are as follows: ZMD, Zoologisk Museum, Copenhagen, Denmark; USNM, National Museum of Natural History, Washington, D.C., U.S.A.; NTM, Northern Territory Museum of Arts and Sciences, Darwin, Australia; AHF, Allan Hancock Foundation, University of Southern California, Los Angeles, California, U.S.A.

Key to the Species of Eastern Pacific Stenopodidean Shrimps

1. Body compressed. Telson narrow, lance-shaped. Endopodite of uropod with two dorsal ridges, a strong median one and a weak inner one, inner ridge with some dorsal hairs, inner ridge sometimes absent. Third maxilliped with long distinct exopodite. ..2
— Body depressed. Telson broad, subquadrangular or subtriangular. Endopodite of uropod with one median dorsal ridge. Third maxilliped with exopodite well developed or absent. 4
2. Carapace and abdomen densely covered with uniformly distributed strong spines arranged in longitudinal rows. Spines erect, curved forward on carapace and first 3 abdominal somites, last 3 abdominal somites with straight posteriorly directed spines. Rostrum with dorsal and lateral spines but no ventral spines. .....*Stenopus hispidus* (Olivier, 1811)
— Abdomen without spines dorsally, carapace with a cincture of spinules along posterior margin of cervical groove (often more parallel cinctures present). Rostrum with dorsal and ventral spines, lateral spines sometimes present. 3
3. Posterior half of carapace, behind cincture of spinules along cervical groove, with distinct transverse row of spinules. Carapace not swollen. Abdominal somites with grooves. .....*Odontozona rubra* Wicksten, 1982
— Posterior half of carapace, behind cincture of spinules along cervical groove, without spinules. Carapace swollen. Abdominal somites without grooves. .....*Odontozona spongicola* (Alcock and Anderson, 1899)
4. Exopodite of second maxilliped present. Third maxilliped with exopodite long and slender, with propodal setiferous organ. First pereiopod with setiferous organ at ventral side of anterior part of carpus and posterior part of propodus. .....*Microprosthema emmiltum* Goy, 1987
— Exopodite of second maxilliped absent. Third maxilliped without exopodite and propodal setiferous organ. First pereiopod without setiferous organ. .....*Spongicoloides galapagensis* Goy, 1980

SYSTEMATICS

Stenopodidae Huxley, 1878

Stenopus Latreille, 1819

Stenopus hispidus (Olivier, 1811) (Fig. 1A)

Restricted synonomy:

Squilla Groenlandica Seba, 1761:54, figs. 6, 7.

Astacus muricatus Olivier, 1791:346.

Penaeus borealis Latreille, 1802:250.

Palaemon hispidus Olivier, 1811:666.—Latreille 1818:5, pl. 319, fig. 2.

Palaemon longipes Latreille, 1818:3, pl. 293, fig. 4.

Stenopus hispidus—Latreille 1819:71; Holthuis 1946:12, pl. I, Figs. a-g; Goy 1987:724.

Material examined.—Male, total length 49.6 mm, ZMD, Pacific Ocean, Taboga, Panama, 8°47'35"N, 79°33'15"W, Th. Mortensen, April 1916.

Diagnosis.—Large shrimp (total length 30–67 mm) with a slender, compressed body, densely covered with spines. Carapace and first three abdominal somites with curved forward-directed spines. Last three abdominal somites with straight posteriorly directed spines. Rostrum strong, ultimate point reaching to about middle of second segment of antennular peduncle with dorsal and lateral spines but no ventral spines. Stylocerite short and pressed against basal antennular segment. Scaphocerite with outer margin entire for considerable distance before final tooth. Third maxilliped with ischium, merus and carpus provided with external row of spinules. Body white with red transverse bands on carapace, third and sixth abdominal somites, and third pereiopods.

Odontozona Holthuis, 1946

Odontozona rubra Wicksten, 1982 (Fig. 1B)

Odontozona rubra Wicksten, 1982:130, figs. 1, 2.—Kerstitch 1989:76, fig. 182.

Odontozona n. sp. Kerstitch, 1984:53.

Material examined.—Female, total length 16.0 mm, holotype, AHF type no. 793, Isla Blanca, off Guaymas, Sonora, Mexico (approximately 27°52'N, 110°52'W), depth 6–9 m, under rocks, Alex Kerstitch, 21 November 1979. Female, total length 20.8 mm, paratype, USNM 184957, Shepard's Rock, Cabo San Lucas, Baja California, Mexico (22°50'N, 109°53'W), depth 5–10 m, cliff, Alex Kerstitch, 26–28 July 1981. Four additional females, total lengths 12.1, 16.1, 16.6, and 17.1 mm (not type material), AHF, Shepard's Rock, Cabo San Lucas, Baja California, Mexico (22°50'N, 109°53'W), depth 5–10 m, cliff, Alex Kerstitch, 26–28 July 1981. Female, total length 9.5 mm, USNM 152360, Gorgona Island, Colombia, 2°58'N, 78°11'50"W, Allan Hancock Expedition #412-35, shallow water, under *Pavona* coral, 22 January 1935.

Diagnosis .—Small shrimp (total length 9.5–20.2 mm) with a slender, compressed body; carapace with few spinules, spinous cincture marking cervical groove; abdominal somites with grooves, no spinules. Rostrum not quite reaching as far as distal end of antennular peduncle, with dorsal, ventral and lateral spines. Stylocerite small, but sharp and distinct. Scaphocerite with concave, serrate outer margin, dorsal surface without spinules. Third maxilliped with few spinules on merus, other segments glabrous. Third pereiopods with segments spinous; other pereiopods glabrous. Posterior margin of telson with two strong lateral teeth and large median tooth. Body translucent with broad red bands on abdomen, red lines on carapace, and red bands on appendages.

Odontozona spongicola (Alcock and Anderson, 1899) (Fig. 1C)

?*Richardina spongicola* Alcock and Anderson, 1899:291.

Richardina spongicola—Alcock 1899:pl. 42, figs. 4, 4a; Alcock 1901:146; Alcock 1902:273.

Odontozona spongicola—Holthuis 1946:40; Holthuis 1955:144, fig. 101b; Wicksten 1982:134.

Material examined.—Female, ovigerous, total length 17.2 mm, AHF, 4.5 miles ENE of Avalon, Santa Catalina Island, California (33°22'26"N, 188°14'55"W–33°22'05"N, 118°14'56"W), depth 604 m, R/V "Velero IV" sta. 1989-50, biological dredge, rocky bottom with worms, echinoderms and mollusks, 12 August 1950. Male, total length 13.1 m, NTM CR000724, 16°18.1'S, 120°18.7'E, depth 496–500 m, R/V "Soela" sta. NWS-67, A. J. Bruce, 5 February 1984.

Diagnosis .—Small shrimp (total length 13.1–26.0 mm) with a slender, compressed body; carapace swollen but thin, with spinous cincture marking cervical groove, second concentric but shorter row of spinules surrounds base of rostrum; rest of carapace and abdomen glabrous. Eyes without pigment. Rostrum strong, almost reaching to end of antennular peduncle, with dorsal spines along entire length, ventral spines on distal third. Few spinules on carpus

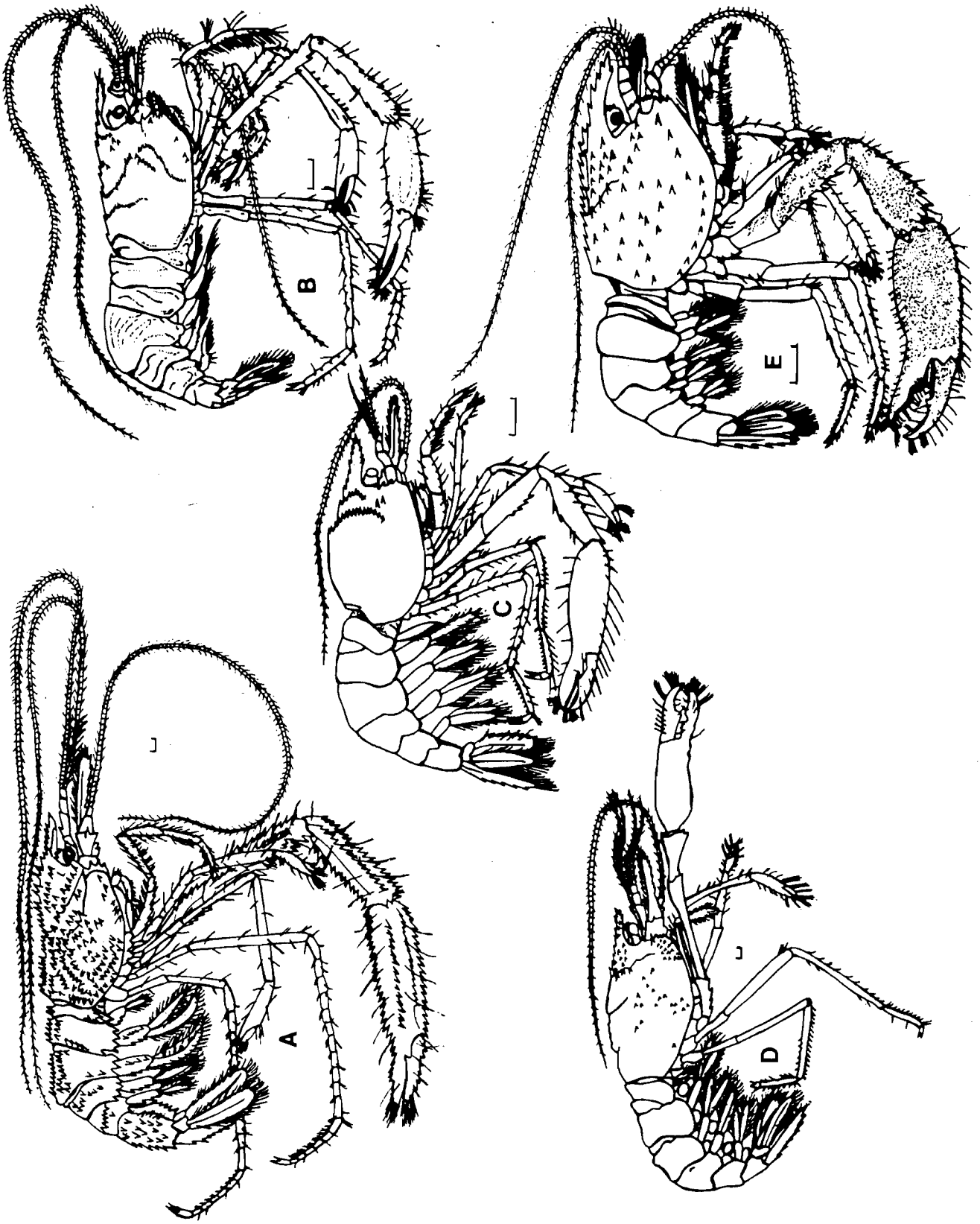

Figure 1. A, *Stenopus hispidus* (after Bate 1888); B, *Odontozona rubra* (after Wicksten 1982); C, *Odontozona spongicola* (NTM CR000724); D, *Spongicoloides galapagensis* (after Goy, 1980); E, *Microprosthema emmiltum* (after Goy 1987). Scale bars, 1.0 mm.

and merus of third pereiopods, rest of pereiopods glabrous. Posterior margin of telson without teeth, except for last two dorsomedian teeth that overlap margin. Color pattern unknown.

Spongicolidae Schram, 1986

Spongicoloides Hansen, 1908

Spongicoloides galapagensis Goy, 1980
(Fig. 1D)

Spongicoloides galapagensis Goy, 1980:760, figs. 1–4.

Material examined.—Female, ovigerous, total length 39.0 mm, holotype, USNM 180064, Galapagos Islands, 00°29'S,89°54'30"W, U.S. Fish Commission Steamer "Albatross" sta. 2818, depth 717 m, white and black sand, large beam trawl, bottom temperature 6.6°C, 15 April 1888.

Diagnosis.—Fairly large shrimp (total length 39.0 m), with stout, depressed body, generally glabrous. Carapace very thin, with distinct cervical groove; less distinct, shorter postcervical groove. Dorsal midline with five small spines anterior to cervical groove and four larger spines posterior to postcervical groove. Eyes without pigment. Rostrum short, compressed, extending almost to distal end of antennular peduncle with strong dorsal and ventral spines and weak lateral spines. Scaphocerite broad, quadrangular, dorsally bearing two faint longitudinal carinae; outer margin with 10 teeth. Third maxilliped with spinous ischium. Third pereiopod with spines on merus and ischium, dorsoventral propodal knobs; other pereiopods glabrous. Telson with six or seven lateral teeth and eight smaller teeth on posterior margin; uropodal exopodite with 13–18 teeth on outer margin, dorsally are strong and one weak ridge. Propodi and carpi of fourth and fifth pereiopods undivided, dactyli triunguiculate. Color pattern unknown.

Microprosthema Stimpson, 1860

Microprosthema emmiltum Goy, 1987
(Fig. 1E)

Microprosthema n. sp. Kerstitch, 1984:53.

Microprosthema emmiltum Goy, 1987:717, figs. 1–4.—Kerstitch 1989:75, fig. 181.

Material examined.—Female, ovigerous, total length 11.7 mm, uncatalogued, Isla San Pedro Martir, Gulf of California, Mexico, 28°39'40"N, 112°35'35"W, depth 13.7 m, under rock, in rubble/sand substrate, Alex Kerstitch, 4 August 1990. Female, ovigerous, total length 11.1 mm, paratype, AHF 8110, Los Frailes, north of Cabo San Lucas, Baja California, Mexico, 23°33'N, 109°24'W, depth 9.1 m, rock and sand, hand net, under rock, Alex Kerstitch, 8 July 1981. Female, ovigerous, total length 14.0 mm, paratype, AHF 161, Taboga Island, Panama, 8°47'35"N, 79°33'15"W, Th. Mortensen, April 1916. Female, total length 14.4 mm, uncatalogued, Bahía de San Lorenzo, Isla Venado (east side), Panama, 8°10'N, 82°10'W, depth 20 m, rock and coral, under dead coral slab, Alex Kerstitch, 27 June 1989. Female, ovigerous, total length 14.3 mm, paratype, USNM 231364, 1°17'38"S, 90°29'55"W, "Velero III" sta. 199-34, W. L. Schmitt, 30 January 1934. Female, total length 17.5 mm, holotype, USNM 231363, Isla Santa Maria (Floreana or Charles Island), Galapagos Islands, off Black Beach, 1°16'36"S, 90°29'42"W, "Velero III" sta. 33-33, rocky shores, W. L. Schmitt, 27 January 1933.

Diagnosis .—Small shrimp (total length 11.1–17.5 mm) with subcylindrical depressed body and few spinous processes; carapace covered with some small spines. Third pereiopods with minutely pitted surface giving scaly appearance; propodus with dorsal crista and numerous small spines dorsally and ventrally. Dorsal surface of abdominal somites glabrous; pleura of last 3 abdominal somites ending in small spines. Dorsal surface of uropodal endopodite with 1–3 spinules outside median ridge. Scaphocerite lobate with 4–5 very strong teeth on outer margin. Antennular and antennal flagella and fourth and fifth pereiopods red, rest of body white, appendages, carapace and abdomen tinged red.

DISCUSSION

The recorded geographic distribution of the five stenopodidean shrimps known from the eastern Pacific is shown in Figure 2. Three species, *Odontozona rubra*, *Microprosthema emmiltum*, and *Spongicoloides galapagensis* are so far known only from the eastern Pacific. The large gap in their distributions along the Mexican and Central American coasts probably can be explained by the lack of collecting in these waters. *Microprosthema emmiltum* shares numerous morphological characteristics with two western Atlantic species, *Microprosthema semilaeve* (Von Martens, 1872) and *Microprosthema manningi* Goy and Felder, 1988. It is an example of a geminate species of decapod crustacean from the eastern Pacific (Abele 1972, 1974). The shallow-water *O. rubra* and *M. emmiltum* are easily overlooked owing to their very small size and cryptic behavior. The lack of sampling of deep shelf waters of tropical regions worldwide as well as in the eastern Pacific is no doubt the principal reason why so few stenopodid commensals of glass sponges have been collected. With adequate sampling of deep water in the eastern Pacific, I expect additional species of *Spongicoloides*, *Spongicola*, and *Spongiocaris* will be found. Interestingly, all specimens of eastern Pacific stenopodids so far collected are female, except for the male *Stenopus hispidus* from Taboga Island.

Odontozona spongicola has a disjunct distribution in the Indo-Pacific. It was known only from the type material (two specimens) dredged in the Andaman Sea and off the Travancore coast, Indian Ocean (Alcock and Anderson 1899, Alcock 1901) and the one specimen collected off Santa Catalina Island, California (Wicksten 1982). I have examined a fourth specimen of this species taken from a hexactinellid sponge off the northwest shelf of Australia (Northern Territory Museum CR000724, Darwin, Australia). This type of disjunct Indo-Pacific distribution has been reported for other marine invertebrates, such as some gastropod mollusks (Kay, 1976), and has been explained by drastic ecological changes causing massive extinctions in parts of the species' range (Fleming 1979). However, since *O. spongicola* is found in a depth range of 496–911 m, a more suitable explanation may be that proposed by Gore (1985) for some Caribbean abyssobenthic caridean shrimp. He suggested that some deep-sea genera of decapod crustaceans may be relatively old and speciate slowly. Isolation of shrimp populations in deep sea basins would be expected to produce minor morphological variation that has lead to some taxonomic confusion at the species level. Gore (1985) felt the concept of geminate species, shown to hold for forms of shallower water, might be applicable to deep-sea forms as well. In the deep sea, the barrier would seem to be distance, which, even if crossed, would result in relatively little morphological change owing to postulated gene flow and slow rates of speciation.

With the record in the eastern Pacific, the distribution of *Stenopus hispidus* is almost circumtropical, although it has not yet been found in the eastern Atlantic (Holthuis 1946). *Stenopus hispidus* is another example of a species that has successfully crossed the East Pacific Barrier (Ekman 1953), much like some caridean shrimps that are found in the Indo-West Pacific region and also in the eastern Pacific region (Bruce 1979). The ability of larvae derived from adult shrimps in the Indo-West Pacific to postpone metamorphosis and settlement and survive may well have been important to colonization of the Galapagos Islands and the tropical eastern Pacific (Holthuis 1951, Bruce 1970). From on their larval

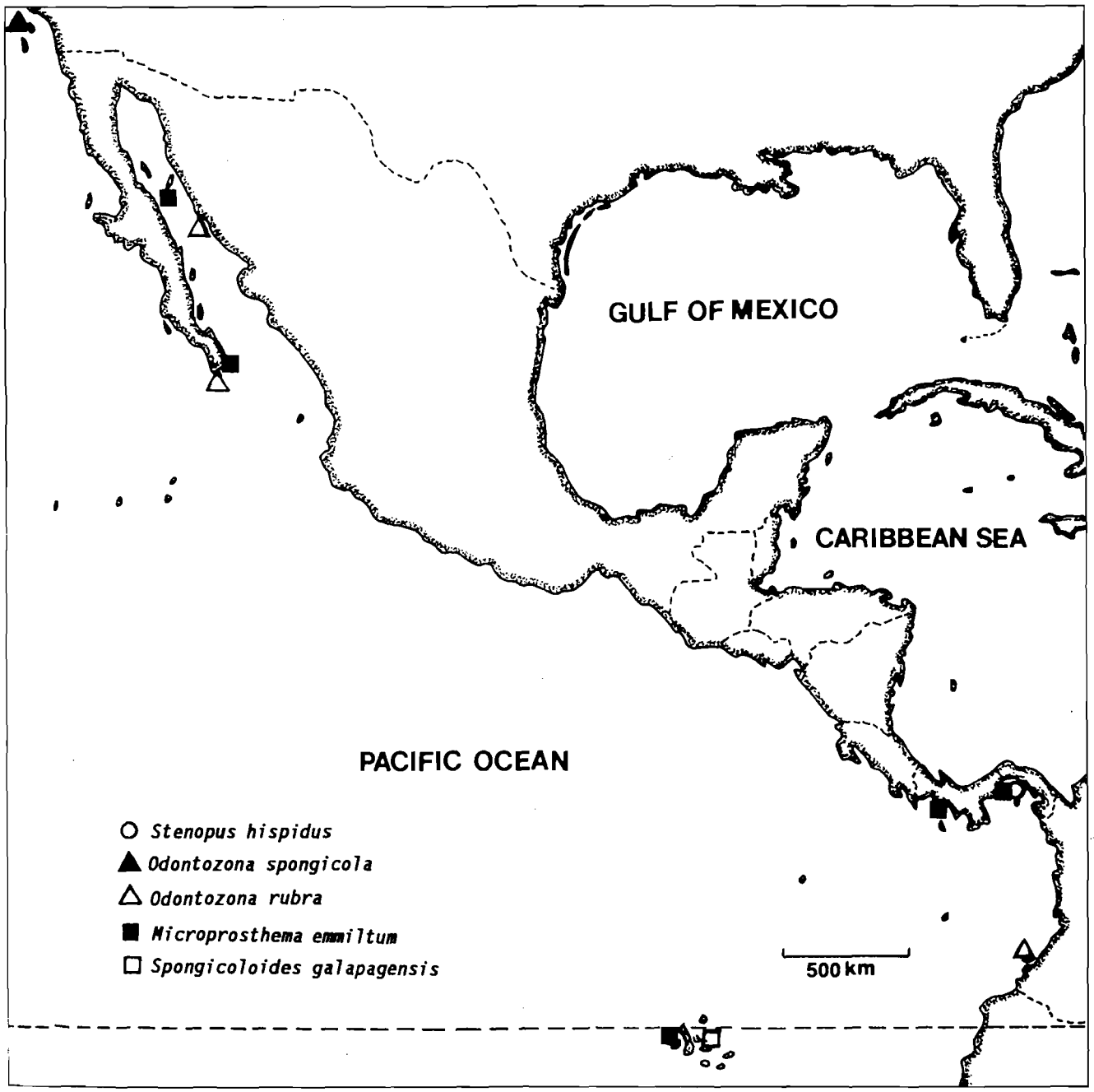

Figure 2. Geographic distribution of stenopodidean shrimps in the eastern Pacific.

developmental patterns other shallow-water stenopodidean shrimps that may be capable of crossing the East Pacific Barrier are *Stenopus tenuirostris* DeMan, 1888, *Stenopus pyrsonotus* Goy and Devaney, 1980, *Stenopus zanzibaricus* Bruce, 1976, *Odontozona sculpticaudata* Holthuis, 1946, and *Microprosthema validum* Stimpson, 1860 (Goy, unpublished observations).

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