The Distributional Ecology and Zoogeographical Relationships of Stomatopod Crustacea from Pacific Costa Rica

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ABSTRACT

Reaka, Marjorie L., and Raymond B. Manning. The Distributional Ecology and Zoogeographical Relationships of Stomatopod Crustacea from Pacific Costa Rica. *Smithsonian Contributions to the Marine Sciences*, number 7, 29 pages, 4 tables, 1980.—Twenty species of stomatopod crustaceans, primarily shallow-water forms, are recorded from Costa Rican localities. Earlier records for size, depth distribution, habitat, and latitudinal distribution are summarized for each species. Habitat use and co-occurrence of species are analyzed, and the zoogeographical relationships of East Pacific species are discussed.

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Introduction

The biota of the East Pacific region is relatively poorly known, despite its considerable zoogeographic significance. The East Pacific has been separated from the West Atlantic region since the late Miocene (Durham and Allison, 1960; Woodring, 1966), and, although high levels of endemism are found there, many East Pacific species show affinities to taxa in the West Atlantic (Woodring, 1966; Briggs, 1974; Manning, 1977; Emerson, 1978). However, some East Pacific species are more closely related to taxa in the East Atlantic than to those in the West Atlantic. For example, a xanthid crab, *Nanocassiope melanodactyla* (A. Milne-Edwards, 1867), is known from the East Pacific and East Atlantic but not from the West Atlantic (Chace, 1966). The closest relatives of five species of East Pacific xanthid crabs (some of them restricted to the Galapagos) occur in the East Atlantic (Garth, 1968). One stomatopod crustacean, *Squilla aculeata*, is represented by subspecies in the East Pacific and East Atlantic but not the West Atlantic; and species in several other East Pacific stomatopod genera (*Eurysquilla*, *Coronida*, *Lysiosquilla*, and *Pseudosquillopsis*) show closest affinities to species in the East Atlantic (Manning, 1977). On the other hand, some species of mollusks occur in the Atlantic and Indo-West Pacific, but not the East Pacific (see Woodring, 1966; Emerson, 1978). Species of four stomatopod genera (*Bathysquilla*, *Odontodactylus*, *Alima*, *Pseudosquilla*) are present in the West Atlantic and Indo-West Pacific, but not in the East Pacific (Manning, 1969a; Manning and Struhsaker, 1976). An alpheid shrimp, *Alpheus paracrinitus* Miers, 1881, is known from the Indo-West Pacific, Clipperton Island in the East Pacific, and the East Atlantic, but does not occur on the East Pacific mainland or in the West Atlantic (Chace, 1962).

The fauna of the offshore islands in the East Pacific (Isla Guadalupe, Islas Tres Marias, Islas de Revillagigedo, Clipperton, Clarion, Cocos, and the Galapagos) is particularly interesting, inasmuch as Indo-West Pacific species often occur in relatively high proportions there but not on the mainland. Of 24 species of nonbrachyuran decapod crustaceans found on Clipperton Island (Chace, 1962), 14 (58%) are known from other

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offshore islands and the Indo-West Pacific. Of these 14 species, six do not extend beyond the offshore islands, four reach the East Pacific mainland, and four occur also in the Atlantic. The remaining 10 species are restricted to the East Pacific, and three of them are endemic to the offshore islands. Of 34 species of brachyuran decapods found on Clipperton, 15 (44%) occur also in the Indo-West Pacific; eight of these species occur only as far east as the offshore islands (Clipperton), and seven reach the mainland. The remaining 19 species occur only in the East Pacific (Garth, 1965, 1974). In the Galapagos, Garth (1946) found 120 species of brachyurans; five (4%) occur also in the Indo-West Pacific, 18 are endemic to the Galapagos, and most of the remaining species occur only in the East Pacific; either the same or the closest relatives of four species occur in the West Atlantic. Of nearly 3400 mollusks in the East Pacific, only 48 (ca. 1%) have Indo-West Pacific affinities. However, except for the rare occurrences of 10 of them on the mainland, 79% of the species with Indo-West Pacific affinities are restricted to the offshore islands (Emerson, 1978). The incidence of Indo-West Pacific elements in the molluskan fauna of the Islas de Revillagigedo (3%), Cocos (7%), and the Galapagos (5%) is lower than that for Clipperton (60%) (Briggs, 1974). Vermeij (1978) has characterized some of the biological attributes of mollusks that do and do not cross this offshore barrier. Also, relatively high proportions of Indo-West Pacific species are found on the offshore islands for corals (56% Cocos, 22% Galapagos) and fishes (23% Islas Revillagigedo, 26% Clipperton and Cocos, 12% Galapagos) (Briggs, 1974). Indo-West Pacific fishes occupy localized coral habitats in the Golfo de Chiriquí, Panama, and similar outposts near Nayarit and Cabo San Lucas, Mexico, as well. However, even in these localities, Indo-West Pacific fishes appear to be less abundant than endemic species (Rosenblatt, McCosker, and Rubinoff, 1972). Like the brachyurans, a number of endemic fishes from the Galapagos are more closely related to species in the West Atlantic than to those in mainland East Pacific areas (Briggs, 1974).

In summary, most East Pacific species are related to other taxa in their region or in the West Atlantic. Some species, however, particularly those from outlying areas of the East Pacific, most closely resemble species from the Atlantic (sometimes the eastern West Atlantic or the East Atlantic), providing a distributional hiatus in mainland East Pacific and/or Caribbean regions. Furthermore, a number of species occur in Atlantic and Indo-West Pacific regions, but not in the East Pacific. Although a number of Indo-West Pacific migrants cross the East Central Pacific expanse to the offshore islands, few traverse the relatively minor remaining distances to the mainland. These faunal relationships obviously raise questions about patterns of habitat use and evolutionary processes along East Pacific shores.

Herein we present an annotated list of the shallow-water stomatopod Crustacea collected during the R/V *Searcher* Expedition to the Pacific coast of Costa Rica in 1972, of which one of us (M.L.R.) was a member. Stomatopods are active predators that occupy burrows in mud, sand, coral, and under rocks, and are important components of tropical communities both in numbers of individuals and in potential impact upon prey species (Abele, 1972, 1974; personal observation). A raptorial appendage is used to hammer and spear prey, to fight other stomatopods, and for defense against predators. Severe, potentially lethal fights erupt among individuals of the same and other species of mantis shrimps; this intense aggression appears to be related to defense of the burrow (Caldwell and Dingle, 1975). In spite of behavior characteristic of intense competition, we know relatively little about the frequency of species exclusion or co-occurrence in these pugnacious predators. Furthermore, we have only meager knowledge about the range of habitats occupied by particular taxa. Such information is critical for interpretation of behavioral studies (reported elsewhere; Reaka and Myers, manuscript in preparation). Also, patterns of local distribution and habitat use shed light on ecological and

TABLE 1.—Collections of stomatopods from the Pacific coast of Costa Rica (station numbers refer to the R/V *Searcher* data log, Cruise 72-3, Costa Rica, Chief Scientist W. A. Bussing, Universidad de Costa Rica)

Station	*Date (1972)*	*Locality*	*Species*	*Habitat and notes*	*Collecting method*
447	9 Mar	Bahia Herradura 9°38′45″N, 84°40′-55″W	*Gonodactylus bahiahondensis* *G. costaricensis*	20 m, tip of outer reef, mud, shell, rocks, little if any coral, sand pockets, surge	ichthyocide, SCUBA
450	10 Mar	same as Sta 447	*G. albicinctus* *Meiosquilla oculinova* squillid postlarva	17 m, side of outer reef, habitat same as station 447	same
451	10 Mar	Bahia Herradura 9°38′50″N, 84°40′-50″W	squillid larva squillid postlarva	37 m, across mouth of bay, mud	15′ otter trawl
455	10 Mar	Bahia Herradura 9°39′30″N, 84°42′-05″W	*Squilla panamensis*	55 m, offshore from Bahia Herradura, mud	
462	11 Mar	near Punta Quepos 9°22′43″N, 84°09′-41″W	*M. swetti* *Heterosquilla mccullochae*	21 m, large porous rubble	ichthyocide, SCUBA
464	12 Mar	Isla Salera (near Punta Quepos) 9°22′12″N, 84°09′-15″W	*M. oculinova* *G. stanschi* *G. bahiahondensis* *G.* sp. juveniles	17 m, rocks	same
471	14 Mar	Isla del Caño 8°43′15″N, 83°53′-07″W	*M. oculinova* *G. bahiahondensis* *G. stanschi* *G. zacae* *G. costaricensis* *G. albicinctus* *Nannosquilla californiensis* *H. mccullochae*	9 m, sand, coral, rubble	same
472	14 Mar	Isla del Caño (same as Sta 471)	*G. zacae* *G. bahiahondensis* gonodactylid larva *M. oculinova* *M. swetti* *H. mccullochae* *Acanthosquilla biminiensis* *Nannosquilla canica*	15 m, pinnacle with rocks and coral rubble, sand around base, lysiosquillids from sand, others from rubble	same
–	–	Isla del Caño	*G. zacae* *G. festae* *G. bahiahondensis* *G. stanschi* *G. costaricensis* *Gonodactylus* juveniles *M. oculinova*	intertidal pool, in and under coral rubble and basalt boulders	collected by hand
482	17 Mar	Isla del Caño 8°43′10″N, 83°54′-30″W	*G. zacae*	37 m, reef pinnacle 1.5 mi from island, rocks and coral rubble	ichthyocide, SCUBA
483	17 Mar	near Isla del Caño	*A. biminiensis*	20 m, lee of island, sandy bottom	same

TABLE 1.—continued

Station	*Date (1972)*	*Locality*	*Species*	*Habitat and notes*	*Collecting method*
484	17 Mar	near Isla del Caño 8°44′20″N, 83°53′-20″W	squillid postlarva	62 m, mud, poor yield of other animals	30′ otter trawl
485	17 Mar	near Isla del Caño 8°46′35″N, 83°54′-00″W	*Pseudosquillopsis marmorata* *Parasquilla similis* *Squilla aculeata* *Cloridopsis dubia*	73 m, mud	same
–	–	near Isla del Caño	*Lysiosquilla desaussurei*	surface	hand net at night light
487	18 Mar	Isla del Caño 8°43′15″N, 83°53′-20″W	*G. zacae* *M. oculinova* *M. swetti*	9 m, lee of island, rock, sand, coral rubble, some surge	ichthyocide, SCUBA
491	19 Mar	Isla del Caño 8°42′55″N, 83°54′-00″W	*G. zacae* *G. bahiahondensis* *G. costaricensis* *M. oculinova*	20 m, pinnacle at corner of island close to shore, rock outcrop	same
–	–	same	*G. zacae* *G. bahiahondensis* *H. mccullochae* *M. oculinova* squillid larva	10–15 m, lee side of island, surge, rock, sand, coral rubble	same
497	20 Mar	Puerto Jiminez	*M. dawsoni*	intertidal mudflat, freshwater stream at low tide	ichthyocide, collected by hand
500	21 Mar	Golfo Dulce 8°28′30″N, 83°12′-45″W	*Squilla panamensis*	55 m, near mouth of gulf, mud	30′ otter trawl

evolutionary processes, and thus on faunal affinities, in different geographic regions.

In this account we also provide a list of all currently recognized species and subspecies of Stomatopoda from the East Pacific. This is followed by an analysis of the distribution patterns and biology of the species collected along the Pacific coast of Costa Rica during the *Searcher* expedition. Then, overall patterns of habitat use and co-occurrence of species in these collections are discussed. Lastly, we discuss the zoogeographical relationships of the East Pacific stomatopods as currently understood.

METHODS AND COLLECTING SITES.—Station data, including localities, habitat characteristics, collecting methods, and species taken at each station, are given above (Table 1). Coordinates for localities mentioned in the text are listed in the Appendix: Gazetteer. For each species, the paragraph on range gives the coordinates for the northern- and southernmost localities; in these paragraphs coordinates from original station data or station data in the literature are not set off in brackets, whereas those coordinates added by us are indicated with brackets. All of the specimens have been deposited in the National Museum of Natural History, Smithsonian Institution, using the abbreviation USNM (the former United States National Museum).

Measurements given in the species accounts with numbers of specimens are rounded off to the nearest half millimeter.

Authors and dates accompanying specific names in the text are considered to be part of the

name, not literature citations. We do not necessarily give original references in the species accounts below, nor do we give complete synonymies. For the older species, original references can be found in the accounts of Schmitt (1940) and Manning (1972a). Original references for species described since 1972 are in the Literature Cited.

ACKNOWLEDGMENTS.—Participation in the *Searcher* cruise was made possible by a grant from the Janss Foundation. During the cruise, led by Chief Scientist William A. Bussing, John McCosker and Richard Rosenblatt collected stomatopods from deeper habitats by diving. We thank Roy L. Caldwell, University of California, Berkeley, for reading the manuscript and for sharing his field observations on stomatopods with us, and Horton H. Hobbs, Jr., Smithsonian Institution, for critically reviewing the manuscript.

Checklist of East Pacific Stomatopoda

Our knowledge of the East Pacific stomatopod fauna has increased greatly in the past few years. The number of species now reported from that region is almost double that reported by Schmitt (1940), 29 species and subspecies representing six genera. Now 50 species and subspecies representing 18 genera have been recorded.

Two species are now known to have been erroneously reported from the East Pacific, the Indo-West Pacific *Lysiosquilla maculata* (Fabricius, 1793) and the West Atlantic *Gonodactylus oerstedii* Hansen, 1895. Both were included in the East Pacific fauna by Schmitt (1940) and by Manning (1972a) in keys to the East Pacific species.

Records of *Lysiosquilla maculata* appear to be based on the similar *L. panamica* Manning, 1971. Those of *Gonodactylus oerstedii* are based on several species, all distinct from that West Atlantic form. Records for *G. oerstedii* from the Gulf of California (Lunz, 1937:4; Schmitt, 1940:211; Steinbeck and Ricketts, 1941:428) appear to be based on *G. stanschi* or *G. zacae*; those of *G. oerstedii* from the Galapagos Islands (Schmitt, 1940:211) are based, at least in part, on *G. pumilus*. All of these collections need to be reexamined.

In addition, records of *Coronida bradyi* (A. Milne Edwards, 1869) (Schmitt, 1940:202; and Manning, 1972a:98, key) are based on the misidentification of the related *Coronida schmitti* Manning. Holthuis (1967:6) included references to *C. schmitti* under *C. armata* (Leach, 1817).

The following Stomatopoda are now known from the East Pacific (* = species reported herein).

Family EURYSQUILLIDAE Manning, 1977
- *Eurysquilla solari* Manning, 1970
- *Eurysquilla veleronis* (Schmitt, 1940)

Family GONODACTYLIDAE Giesbrecht, 1910
- **Gonodactylus albicinctus* Manning and Reaka, 1979
- **Gonodactylus bahiahondensis* Schmitt, 1940
- **Gonodactylus costaricensis* Manning and Reaka, 1979
- **Gonodactylus festae* Nobili, 1901
- *Gonodactylus lalibertadensis* Schmitt, 1940
- *Gonodactylus pumilus* Manning, 1970
- **Gonodactylus stanschi* Schmitt, 1940
- **Gonodactylus zacae* Manning, 1972

Family LYSIOSQUILLIDAE Giesbrecht, 1910
- **Acanthosquilla biminiensis* (Bigelow, 1893)
- *Acanthosquilla digueti* (Coutière, 1905)
- *Coronida glasselli* Manning, 1976
- *Coronida schmitti* Manning, 1976
- *Heterosquilla insolita* (Manning, 1963)
- **Heterosquilla mccullochae* (Schmitt, 1940)
- *Heterosquilla polydactyla* (von Martens, 1881)
- **Lysiosquilla desaussurei* (Stimpson, 1857)
- *Lysiosquilla panamica* Manning, 1971
- *Nannosquilla anomala* Manning, 1967
- **Nannosquilla californiensis* (Manning, 1961)
- **Nannosquilla canica* Manning and Reaka, 1979
- *Nannosquilla chilensis* (Dahl, 1954)
- *Nannosquilla decemspinosa* (Rathbun, 1910)
- *Nannosquilla galapagensis* Manning, 1972
- *Nannosquilla similis* Manning, 1972
- *Neocoronida cocosiana* (Manning, 1972)

Family PSEUDOSQUILLIDAE Manning, 1977
- *Hemisquilla ensigera californiensis* Stephenson, 1967
- *Hemisquilla ensigera ensigera* (Owen, 1832)
- **Parasquilla similis* Manning, 1970
- *Pseudosquilla adiastalta* Manning, 1964
- *Pseudosquillopsis lessonii* (Guérin, 1830)
- **Pseudosquillopsis marmorata* (Lockington, 1877)

Family SQUILLIDAE Latreille, 1803
- *Clorida mauiana* (Bigelow, 1931)
- **Cloridopsis dubia* (H. Milne Edwards, 1837)
- **Meiosquilla dawsoni* Manning, 1970
- **Meiosquilla oculinova* (Glassell, 1942)
- **Meiosquilla swetti* (Schmitt, 1940)

Pterygosquilla armata armata (H. Milne Edwards, 1837)
Pterygosquilla gracilipes (Miers, 1881)
Schmittius peruvianus Manning, 1972
Schmittius politus (Bigelow, 1891)
**Squilla aculeata aculeata* Bigelow, 1893
Squilla biformis Bigelow, 1891
Squilla bigelowi Schmitt, 1940
**Squilla hancocki* Schmitt, 1940
Squilla mantoidea Bigelow, 1893
**Squilla panamensis* Bigelow, 1891
Squilla parva Bigelow, 1891
Squilla tiburonensis Schmitt, 1940

In addition to the 20 species listed above as occurring off Costa Rica, five other species have been previously recorded from the area:

Gonodactylus lalibertadensis Schmitt: Reported from Puerto Culebra and Uvita Bay by Manning (1972a:111); these specimens should be reexamined, as they could actually be *G. costaricensis* (see below). However, two other specimens (♂ 25 mm, ♀ 35 mm; USNM 168629; from Isla San Lucas) in the Smithsonian collections are clearly identifiable with Schmitt's species.

Nannosquilla decemspinosa (Rathbun): Recorded from Isla San Lucas, Golfo de Nicoya, and Playa Blanca by Schmitt (1940:189) and Manning (1961:30). Two of the three Costa Rican specimens mentioned by these authors were identified correctly; the third proved to be identifiable with *Nannosquilla canica* (see below).

Pseudosquilla adiastalta Manning: Recorded from Port Parker and Isla Jasper by Manning (1972a:106).

Squilla bigelowi Schmitt: Reported from Puntarenas by Boone (1930:39) as *S. panamensis* var. B and corrected to *S. bigelowi* by Schmitt (1940: 157) and Manning (1967b:104).

Squilla parva Bigelow: Reported from Puerto Culebra by Manning (1972a:104).

Family GONODACTYLIDAE Giesbrecht, 1910

Gonodactylus albicinctus Manning and Reaka, 1979

Gonodactylus albicinctus Manning and Reaka, 1979:634, fig. 1.

MATERIAL.—BAHIA HERRADURA: Sta 450, 17 m: 1♂ 25 mm, 1♀ 19 mm. ISLA DEL CAÑO: Sta 471, 9 m: 1♀ 13 mm.

PREVIOUS COSTA RICAN RECORDS.—Bahia Herradura and Isla del Caño (Manning and Reaka, 1979).

RANGE.—East Pacific: known only from the Costa Rican localities listed above.

HABITAT.—Subtidal: mud, shell, and rocks, 17 m; sand, coral rubble, 9 m (Manning and Reaka, 1979).

SIZE.—1♂ 25 mm; 2♀ 13–19 mm.

COMMENTS.—*Gonodactylus albicinctus* is closely related to *G. bahiahondensis* but differs in morphological features and in color in life as well. This species has a white rather than powder-blue meral spot and the body is marked with a conspicuous white band across the sixth abdominal somite. This species is rather small and was found only in moderately deep sublittoral habitats.

Gonodactylus bahiahondensis Schmitt, 1940

Gonodactylus oerstedii var. *festae*.—Bigelow, 1931:124 [part], pl. 2: figs. 3, 4 [not *Gonodactylus festae* Nobili, 1901].
Gonodactylus bahiahondensis Schmitt, 1940:217, fig. 31.—Manning, 1972a:111; 1974:102; 1976a:223.

MATERIAL.—BAHIA HERRADURA: Sta 447, 20 m: 1♂ 19 mm. ISLA SALERA: Sta 464, 17 m: 2♀ 10.5–12 mm. ISLA DEL CAÑO: Sta 471, 9 m: 2♂ 32–32.5 mm; Sta 472, 15 m: 1♂ 34 mm; –, intertidal: 7♂ 17–28 mm, 13♀ 8–38 mm; Sta 491, 20 m: 1♂ 19 mm; –, 10–15 m: 1♂ 17 mm.

PREVIOUS COSTA RICAN RECORDS.—Puerto Culebra (Schmitt, 1940; Manning, 1972a). Port Parker (2 stations); Isla Jasper; Uvita Bay (Manning, 1972a).

RANGE.—East Pacific: Port Parker, Costa Rica [10°56′N, 85°49′W] to Isla La Plata, Ecuador, 01°15.5′S, 81°05′W. Mainland and nearshore islands.

HABITAT.—Intertidal and shallow sublittoral, including: coral clumps (Schmitt, 1940); in coral, under stone at low tide (Manning, 1972a); on sand, on coral, 7–9 m (Manning, 1974); bedrock, boulders, gravel, sand, 6–9 m; coral, sand, rubble, detritus, 11–13 m; branching coral, some coral heads, 5–6 m; silt, coral stacks, debris, 3–6 m (Manning, 1976a); mud, shell, sand, and rock;

rocks; rock and rubble; coral rubble; 0–20 m (this study).

SIZE.—1♀ 34 mm (Bigelow, 1931); 1♀ 43 mm (Schmitt, 1940); 5♂ 18–36 mm, 9♀ 22–41 mm (Manning, 1972a); 1♂ 26 mm, 2♀ 41–49 mm (Manning, 1974); 5♂ 12–41 mm, 5♀ 29–40 mm, 4 juvs 7 mm (Manning, 1976a); 13♂ 17–32.5 mm, 15♀ 8–38 mm (this study). Overall size range of males 12 to 41 mm, of females 8 to 49 mm.

COMMENTS.—This species was one of the most common gonodactylids in terms of both numbers of localities frequented and individuals found in this study. *Gonodactylus bahiahondensis* occurs from intertidal to 20 m, and commonly is found in coral rubble and associated debris; however, it also has been recorded on rocky and sand substrates in the absence of coral. Juveniles as small as 7 mm have been identified, and individuals may reach 49 mm in length (24♂, 35♀). Among the best identifying characteristics are the armored bilobed knob on the oerstedii-type telson (see Manning, 1969a) and the spiniform rostrum, which are visible even on small individuals. In this study, body color of live individuals ranged from dark red to brown, purple, and green, and the species-specific meral spot used in displays of the raptorial appendage was powder blue.

Gonodactylus costaricensis Manning and Reaka, 1979

Gonodactylus lalibertadensis.—Manning, 1972a:111 [not *Gonodactylus festae lalibertadensis* Schmitt, 1940].

Gonodactylus costaricensis Manning and Reaka, 1979:636, fig. 2.

MATERIAL.—BAHIA HERRADURA: Sta 447, 20 m: 2♀ 35 mm. ISLA DEL CAÑO: Sta 471, 9 m: 1♀ 32 mm; –, intertidal: 4♀ 25–34 mm; Sta 491, 20 m: 1♀ 30 mm.

PREVIOUS COSTA RICAN RECORDS.—Puerto Culebra; Uvita Bay (Manning, 1972a). Bahía Herradura; Isla del Caño (Manning and Reaka, 1979).

RANGE.—East Pacific: known only from the Costa Rican localities listed above.

HABITAT.—Intertidal and shallow sublittoral, including: coral (Manning, 1972a); mud, shell, rocks, 20 m; sand, coral rubble, 9 m; intertidal coral rubble and boulders; rocks, 20 m (Manning and Reaka, 1979).

SIZE.—Females only known: 2♀ 27–37 mm (Manning, 1972a); 8♀ 25–35 mm (Manning and Reaka, 1979).

COMMENTS.—Although we have not reexamined the material reported by Manning (1972a) as *Gonodactylus lalibertadensis*, we suspect that it is a member of *G. costaricensis* rather than *G. lalibertadensis*; in Table 5 (p. 110) Manning indicated that his specimen had one row of spines on the submedian teeth of the telson, a characteristic of *G. costaricensis*. *Gonodactylus costaricensis* is closely related to *G. lalibertadensis*, known from Ecuador, Panama, and Costa Rica, as noted above (Schmitt, 1940; Manning, 1972a, 1974). However, in Panama *G. lalibertadensis* has a white meral spot (R. L. Caldwell, personal communication), whereas the meral spots are powder blue in *G. costaricensis*. Body color of this chromatophore-speckled species ranges from scarlet or mottled brown to emerald. *Gonodactylus costaricensis* occurs in a variety of habitats from the intertidal to a depth of 20 m, and is of modest body size and aggressive level.

Gonodactylus festae Nobili, 1901

Gonodactylus festae.—Schmitt, 1940:220, fig. 32.—Manning, 1972a:110.

Gonodactylus festai.—Manning, 1974:102 [unjustified emendation].

MATERIAL.—ISLA DEL CAÑO: –, intertidal: 5♂ 15–35 mm, 10♀ 21–39 mm.

PREVIOUS COSTA RICAN RECORDS.—Bahía de Salinas (Schmitt, 1940). Port Parker; Bahía Carrillo [Piedra Blanca Bay] (Manning, 1972a). Puntarenas (Manning, 1974).

RANGE.—East Pacific: Golfo de Fonseca, El Salvador [13°10′N, 87°40′W] to Bahía de Santa Elena, Ecuador [02°06′S, 80°53′W]. Mainland and nearshore islands.

HABITAT.—Intertidal and shallow sublittoral, including: shore; beach beyond reef; sand, stone (Schmitt, 1940); tidepool; under stone, low tide

(Manning, 1972a); mud and detritus, intertidal to 15 m (Panama, R. L. Caldwell, pers. comm.); intertidal coral rubble and basalt boulders (this study).

SIZE.—2♀ 43–49 mm (Schmitt, 1940); 3♂ 38–44 mm (Manning, 1972a); 1♂ 31 mm, 4♀ 20–37 mm (Manning, 1974); 5♂ 15–35 mm, 10♀ 21–39 mm (this study). Overall size range of males 15 to 44 mm, of females 20 to 49 mm.

COMMENTS.—Although *Gonodactylus festae* is recorded from relatively few localities, this species reaches comparatively high densities in local habitats, as indicated in the site at Isla del Caño in this study, and particularly in the Gulf of Panama, where it is the most abundant shallow-water gonodactylid (R. L. Caldwell, personal communication). In contrast to the other gonodactylids, *G. festae* occurs predominantly in shallow water (0–15 m, and collected only intertidally in this study). Although in this study *G. festae* occurred only in coral rubble among boulders, it has been recorded from sandy, muddy, and rocky habitats in other localities. Body color of live individuals from Costa Rica was mottled brown, and the meral spot was deep pink. Compared to other East Pacific gonodactylids, the oerstedii-type telson of *G. festae* is broad and heavily armed with carinae and spines. This species showed significantly more aggression toward other gonodactylids than any other Costa Rican species (M.L.R., personal observation), and preserved specimens frequently show damage and regenerative repair, presumably from wounds incurred in fights (R.B.M., personal observation).

Gonodactylus stanschi Schmitt, 1940

Gonodactylus stanschi Schmitt, 1940:215, fig. 30.—Steinbeck and Ricketts, 1941:429.—Manning, 1972a:110.

MATERIAL.—ISLA SALERA: Sta 464, 17 m: 2♀ 11–11.5 mm. ISLA DEL CAÑO: Sta 471, 9m: 1♀ 13 mm; –, intertidal: 2♂ 10–15 mm, 1♀ 14 mm.

PREVIOUS COSTA RICAN RECORDS.—None.

RANGE.—East Pacific: Gulf of California, from Isla Angel de la Guarda, Mexico [29°20′N, 113°25′W] to Isla del Caño, Costa Rica, 08°43′-15″N, 83°53′07″W, including Isla Isabela and Islas Tres Marias, Mexico. Mainland and nearshore islands.

HABITAT.—Intertidal and shallow sublittoral, including: coral banks, oyster beds (Schmitt, 1940); in coral, and in coral, 2.7 m (Manning, 1972a); rocks; rocks and coral rubble; sand and coral rubble; intertidal to 17 m (this study).

SIZE.—1♀ 38 mm (Mexico, Schmitt, 1940); 4♂ 19–36 mm, 9♀ 12–41 mm (Mexico, Manning, 1972a); 2♂ 10–15 mm, 4♀ 11–14 mm (this study). Overall size range of males 10 to 36 mm, of females 11 to 41 mm.

COMMENTS.—*Gonodactylus stanschi* is a relatively northern species, in comparison with other East Pacific *Gonodactylus*, and all of the individuals collected in Costa Rica were small (≤15 mm). It is known to reach 41 mm in length in Mexico (6♂, 14♀), and has been recorded from shallow water (0–17 m) with coral rubble.

One of the best identifying characteristics for *G. stanschi* is the rounded, unarmed knob on the oerstedii-type telson. This feature distinguishes even young individuals, such as those found in this study, from those of most other East Pacific species with similar telson shapes. Although the carinae on the telson of *G. stanschi* bear dorsal spines, these are less numerous than for other East Pacific species with armored telsons. Also, as the carinae become inflated in larger individuals, their spines are reduced to increasingly smaller tubercles. This phenomenon is especially apparent in the northern Gulf of California, where *G. stanschi* reaches larger sizes than in more southern localities (personal observations). The lack of spines on the telsons of members of these northern populations has resulted in their erroneous identification in some cases as *G. oerstedii*, otherwise an Atlantic species that does not bear spines on the knob, on the anchor posterior to the median carina, or on the dorsal surfaces of the telson carinae (Manning, 1969a).

Gonodactylus zacae Manning, 1972

Gonodactylus oerstedii.—Schmitt, 1940:211 [part], figs. 27, 28

[not fig. 26 = *G. oerstedii* Hansen, 1895; not fig. 29 = *G. pumilus* Manning, 1970].—Steinbeck and Ricketts, 1941: 428 [not *Gonodactylus oerstedii* Hansen, 1895].

Gonodactylus zacae Manning, 1972a, fig. 3; 1974:103, fig. 1; 1976a:223.

MATERIAL.—ISLA DEL CAÑO: Sta 471, 9 m: 3♂ 22–31.5 mm; Sta 472, 15 m: 2♂ 23.5–25 mm, 3♀ 14–26 mm; –, intertidal: 1♂ 23 mm, 5♀ 16–26.5 mm; Sta 482, 37 m: 1♀ 16 mm; Sta 487, 9 m: 8♂ 18.5–30 mm, 2♀ 24–31 mm; Sta 491, 20 m: 1♀ 28 mm; –, 10–15 m: 1♂ 22 mm.

PREVIOUS COSTA RICAN RECORDS.—Puerto Culebra (Schmitt, 1940). Port Parker (4 stations) (Manning, 1972a).

RANGE.—East Pacific: Gulf of California, from Bahía Concepción, Mexico [26°39′N, 111°48′W] to Isla La Plata, Ecuador, 01°16′S, 81°06′W, including Islas Tres Marias, Islas de Revillagigedo, Clarion Island, and the Galapagos Islands (USNM records). Mainland, nearshore and offshore islands.

HABITAT.—Intertidal and sublittoral shelf, including: sand, algae, 8.2 m; sand, algae, 3.6 m; sand, algae, 5.4 m; gravel, algae, 12.8 m; rocks, dead coral, mud, shells, leaves, 5.4–20 m; shells, algae, 16.4–19.1 m; sand, crushed shell, 6.3 m; rocks, sand, algae, 8.2–11 m; coral, 2.7–7.2 m; coral, 7.3 m; 33 m; 64 m (Manning, 1972a); sand, 7–9 m, sand, 5.5–9 m; 5.5–9 m; 15–18 m; 27 m (Manning, 1974); boulders, talus, debris, 2.4–6.1 m (Manning, 1976a); in coral rubble, 1–10 m (Isla Espirito Santo and Bahía de La Paz, Gulf of California, M.L.R., personal observation); rocks; rocks and coral rubble; sand and coral rubble, 0–37 m (this study).

SIZE.—44♂ 9–36 mm, 36♀ 8–32 mm (Mexico and Costa Rica, Manning, 1972a); 1♂ 41 mm (Mexico); 30♂ 10–29 mm, 26♀ 8–37 mm (Panama, Manning, 1974); 1♀ 22 mm (Ecuador, Manning, 1976a); 86♂ 15–58 mm, 143♀ 16–59 mm (La Paz, Gulf of California, M.L.R., unpublished data); 15♂ 18.5–31.5 mm, 12♀ 14–31 mm (this study). Overall size range of males 9 to 58 mm, of females 8 to 59 mm.

COMMENTS.—Geographically, *Gonodactylus zacae* is the most widespread gonodactylid in the East Pacific, and, along with *Meiosquilla oculinova* and *Gonodactylus bahiahondensis*, was one of the most common species in terms of both localities occupied and numbers of individuals recorded in this study. A habitat generalist, *G. zacae* occupies coral rubble and rock habitats as well as sandy and muddy areas (with debris, shell, or algae, and without rocks and coral); may occur either alone or with other species (no other gonodactylid in this study was collected alone); and has the broadest depth distribution of any gonodactylid in this study (with published records to 64 m, deeper than any other East Pacific *Gonodactylus*). In Pacific Central America, *G. zacae* appears to occur most frequently in habitats of moderate depth (although it was found at one intertidal site on an island). This species reaches high densities in shallow areas in the lower Gulf of California (M.L.R., personal observation). Body size appears to increase at higher latitudes. Recorded individuals from Panama and Costa Rica (59♂, 49♀) do not exceed 37 mm; those from the Gulf of California (87♂, 143♀) reach 59 mm in length. The meral spot in populations from both Costa Rica and the Gulf of California is rose pink. Body color of live specimens in Costa Rica ranged from vermilion to mottled browns and greens. Field notes on one individual indicated "bright red; white specks on the back, white stripes across carapace and merae [sic], carpus of raptorial appendage purple, legs red, uropods red-violet, pleopods red with purple tips." Color of the carpus, legs, uropods, and pleopods did not vary among individuals. Body color of individuals in the lower Gulf of California ranges from mottled brown-black to various shades of green, but red has not been observed. *Gonodactylus zacae* from Costa Rica are less aggressive than *G. festae* or *G. bahiahondensis*, but the large individuals from the Gulf of California show high aggression (M.L.R., personal observation).

The specimens (3♀ 22.5–33.5 mm) from Puerto Culebra reported by Schmitt (1940:211) as *G. oerstedii* are in the Smithsonian collections (USNM 76298). They, like two specimens from the northern Gulf of California collected by E. F. Ricketts (1♀ 41.5, USNM 81339; 1♂ 19.5, USNM 81349), are presumably the basis for the records

of *G. oerstedii* in Steinbeck and Ricketts (1941: 428), and are clearly identifiable with *G. zacae*.

Discussion of Gonodactylidae

The East Pacific gonodactylids appear to derive from an American stock with small ocular scales, rather than from Indo-West Pacific lineages (Manning, 1969a, 1972a). However, all are specifically distinct from their West Atlantic relatives, and both groups of species in turn are distinct from all Indo-West Pacific species. *Gonodactylus zacae* forms one divergent lineage, with rounded anterolateral angles of the rostral plate and a long, triangular bredini-type telson without spines (Manning, 1969a, 1972a). However, *G. zacae* has a broader body and reaches a smaller size (59 mm) than its West Atlantic counterpart, *G. bredini* Manning, 1969 (75 mm; Manning, 1969a). Also, in *G. bredini*, the meral spot, exposed during aggressive and mating displays, is white, whereas that of *G. zacae* is rose pink. The second major lineage includes all of the other East Pacific species of *Gonodactylus* except for the Galapagan *G. pumilus*. These gonodactylids have relatively short, broad oerstedii-type telsons with distinct submedian teeth and dorsal spinules (Manning, 1969a, 1972a). Although the telsons of these species resemble those of *G. oerstedii* Hansen, *G. curacaoensis* Schmitt, 1924, *G. torus* Manning, 1969, *G. austrinus* Manning, 1969, and *G. petilus* Manning, 1970, in the West Atlantic, all of the East Pacific species are distinguished from those in the West Atlantic by the acute and sharp rather than rounded anterolateral angles of the rostral plate. In the West Atlantic, *G. oerstedii* displays a magenta meral spot; both *G. spinulosus* Schmitt, 1924 and *G. curacaoensis* bear white meral spots (M.L.R., personal observation). In the East Pacific, species with oerstedii-type telsons show several colors of meral spots (*G. festae* deep pink, *G. bahiahondensis* and *G. costaricensis* powder blue, *G. albicinctus* white); *G. lalibertadensis*, not recorded in this study, has a white meral spot (R. Caldwell, personal communication). Although invariant among individuals of a species, the color of the meral spot appears to be particularly labile among species within lineages. This variability is most apparent in the morphologically closely related species pairs, *G. zacae* (pink) vs. *G. bredini* (white), *G. festae* (pink) vs. *G. spinulosus* (white), *G. costaricensis* (blue) vs. *G. lalibertadensis* (white), and *G. bahiahondensis* (blue) vs. *G. albicinctus* (white), and *G. oerstedii* (magenta) vs. *G. curacaoensis* (white).

All of the previously known East Pacific species of *Gonodactylus* were collected in this study except for *G. lalibertadensis* (Costa Rica, Panama, Ecuador; Schmitt, 1940, Manning, 1972a, 1974) and *G. pumilus* (Galapagos; Schmitt, 1940, Manning, 1970, 1972a). *Gonodactylus pumilus* is small (8–20 mm, N = 22), has an oerstedii-type telson without spines, and has been taken from coral heads in 5 m. Although most closely related to East Pacific species, *G. pumilus* also resembles a dwarf species in the West Atlantic (*G. torus*, ≤20 mm), which occurs sublittoraly off North Carolina and Florida (Manning, 1969a, 1970). Including the two species newly described from this study (Manning and Reaka, 1979), eight species of *Gonodactylus* are known from the East Pacific. At least nine species of *Gonodactylus* occur in the West Atlantic. Additionally, at least 24 species of *Gonodactylus* are known from Indo-West Pacific regions, and nine genera containing at least 35 species related to *Gonodactylus (Chorisquilla, Echinosquilla, Gonodactylolus, Gonodactylopsis, Haptosquilla, Mesacturus, Mesacturoides, Hoplosquilla,* and *Hoplosquilloides*) also occur in the Indo-West Pacific; only two species of the related genus *Protosquilla* represent the gonodactylids in the East Atlantic. Restricted by the sizes of crevices in rocks and coral which protect them from predation, these gonodactylids all are relatively small (usually less than 100 mm). The postlarvae of *Gonodactylus* also are small (6–9 mm), and the pelagic period lasts only about a month (Manning, 1969a; Provenzano and Manning, 1978).

Gonodactylids are more aggressive and more heavily armored than other stomatopods. This study showed wide overlap in habitat and depth, with highly variable patterns of co-occurrence

among particular species. Competitive exclusion from local habitats did not appear to occur among species of *Gonodactylus* unless this process occurred on a finer scale of micro-habitat segregation than that resolved here. *Gonodactylus festae* occurred in the most restricted habitat and was the most aggressive of the gonodactylids studied, but did not exclude other species from the shallow rubble substrates frequented by it.

Family Lysiosquillidae Giesbrecht, 1910

Acanthosquilla biminiensis (Bigelow, 1893)

Acanthosquilla biminiensis.—Manning, 1969a:63, figs. 14, 15.—Camp, 1973:11, figs. 3, 4.—Manning, 1974:102.

Material.—Isla del Caño: Sta 472, 15 m: 1♀ 38.5 mm; Sta 483 (near Isla del Caño), 20 m: 2♂ 43–56 mm.

Previous Costa Rican Records.—None.

Range.—American. East Pacific: from the nearshore islands of Isla del Caño, Costa Rica, 08°43′15″N, 83°53′07″W, and Isla Taboga [08°47′N, 79°33′W] and Isla Taboguilla [08°-48′N, 79°31′W], Panama. West Atlantic: from scattered localities between Bimini and Brazil, including Gulf of Mexico (Manning, 1969a; Camp, 1973).

Habitat.—Sublittoral. East Pacific: sand, rocks, coral rubble, 15 m; sand, 20 m (this study). West Atlantic: 2–4 m (Manning, 1969a); 7.6–18.3 m (Camp, 1973).

Size.—East Pacific: 9♂ 16–40 mm, 7♀ 24–50 mm (Manning, 1974); 2♂ 43–56 mm, 1♀ 38.5 mm (this study). West Atlantic: 3♂ 39–62 mm (Manning, 1969a); 2♂ 22–49 mm, 1♀ 21 mm, 3 postlarvae 9–10 mm (Camp, 1973). Overall size range of males 16 to 62 mm, of females 21 to 50 mm.

Comments.—Our specimens have a single black spot on the telson, encompassing the median and submedian dorsal spines; in this they resemble specimens previously recorded from the Pacific coast of Panama (Manning, 1974) and Brazil (Manning, 1969a:66) rather than those from Bimini in which there is a pair of submedian dark spots. Two of three adult specimens, one male and one female, from the Gulf of Mexico reported by Camp (1973) have a single spot; the third specimen, a male, has two submedian spots.

Heterosquilla mccullochae (Schmitt, 1940)

Lysiosquilla mccullochae Schmitt, 1940:197, fig. 23.
Heterosquilla (Heterosquilloides) mccullochae.—Manning, 1969a: 55, fig. 12; 1974:105, fig. 2.
Heterosquilla jonesi Shanbhogue, 1971:100.

Material.—Near Punta Quepos: Sta 462, 21 m: 2♂ 45–46 mm. Isla del Caño: Sta 471, 9 m: 1♀ 25 mm; Sta 472, 15 m: 2♂ 19–25 mm; –, 10–15 m: 1♂ 40 mm.

Previous Costa Rican Records.—None.

Range.—Circumtropical. East Pacific: Gulf of California, from Isla San Francisco, Mexico [24°50′N, 110°35′W] to Isla Taboga, Panama [08°47′N, 79°33′W]. Primarily from nearshore islands in the East Pacific. Also West Atlantic, from Florida and Puerto Rico (Manning, 1969a); Central Atlantic, from Ascension Island (R.B.M., unpublished data); and Indian Ocean (Shanbhogue, 1971).

Habitat.—Sublittoral. East Pacific: Coralline algae bottom, 54 m (Schmitt, 1940); sand and coral rubble, 9 m and 21 m; sand, rocks, and rubble, 10–15 m and 15 m (this study). Habitat unknown outside of East Pacific.

Size.—East Pacific: 1♀ 32 mm (Schmitt, 1940); 1♀ 50 mm (Manning, 1974); 5♂ 19–46 mm, 1♀ 25 mm (this study). West Atlantic: 2♀ 21–32 mm (Manning, 1969a). Overall size range of males 19 to 46 mm, of females 21 to 50 mm.

Comments.—*Heterosquilla mccullochae* is the most widely distributed species of stomatopod; it is the only species common to the Atlantic, Indo-West Pacific, and East Pacific regions. Almost nothing is known of its biology. It appears to be an aberrant *Heterosquilla*, and may well have to be placed in a separate genus.

Lysiosquilla desaussurei (Stimpson, 1857)

Lysiosquilla desaussurei.—Del Solar et al., 1970:36.—Manning, 1969a:32; 1972a:99, fig. 2; 1974:106.

Material.—Near Isla del Caño: –, surface: 1♂ 84 mm.

PREVIOUS COSTA RICAN RECORDS.—Bahia Carrillo (Manning, 1972a).

RANGE.—East Pacific: Los Palmillos, San Jose del Cabo, Baja California, Mexico [23°03′N, 109°41′W] to Caleta le Cruz, 03°38′S, near Tumbes, Peru [03°34′S, 80°28′W]. Mainland.

HABITAT.—Sublittoral, 20–48 m (Del Solar et al., 1970). All other recently acquired specimens taken by dip net at night light.

SIZE.—1♂ 210 mm (Manning, 1969a:32); 3♂ 68–86 mm, 1♀ 84 mm (Manning, 1972a); 1♂ 82 mm (Manning, 1974); 1♂ 84 mm (this study). Overall size range of males 68 to 210 mm, of females 84 mm.

COMMENTS.—Almost nothing is known about the biology of this moderately large and geographically widespread but rare species.

Nannosquilla californiensis (Manning, 1961)

Lysiosquilla digueti.—Schmitt, 1940:194 [part, not fig. 22] [not *Lysiosquilla digueti* Coutière, 1905].
Lysiosquilla californiensis Manning, 1961:33, figs. 4–6.

MATERIAL.—ISLA DEL CAÑO: Sta 471, 9 m: 4♂ 17–23 mm, 2♀ 17.5–20.5 mm.

PREVIOUS COSTA RICAN RECORDS.—None.

RANGE.—East Pacific: Gulf of California, from Puerto Escondido, Baja California, Mexico [25°-48′N, 111°20′W] and Isla del Caño, Costa Rica, 08°43′15″N, 83°53′07″W (this study). Mainland and nearshore islands.

HABITAT.—Sublittoral, 48 m (Schmitt, 1940; Manning, 1961); sand and coral rubble, 9 m (this study).

SIZE.—1♂ 20 mm (Schmitt, 1940; Manning, 1961); 4♂ 17–23 mm, 2♀ 17.5–20.5 mm (this study).

COMMENTS.—This species, like *Nannosquilla canica* (below), resembles the more common *N. decemspinosa*, but it can be distinguished readily from both of these by the larger number of marginal projections on the false eave of the telson. Both *N. californiensis* and *N. canica* differ from *N. decemspinosa* in that they live sublittorally rather than in the intertidal zone.

Nannosquilla canica Manning and Reaka, 1979

Lysiosquilla decemspinosa.—Schmitt, 1940:189, fig. 20c [part, not fig. 20a,b].—Manning, 1961:30 [part] [not *Lysiosquilla decemspinosa* Rathbun, 1910].
Nannosquilla canica Manning and Reaka, 1979:637, fig. 3.

MATERIAL.—ISLA DEL CAÑO: Sta 472, 15 m: 2♀ 15–16.5 mm.

PREVIOUS COSTA RICAN RECORDS.—Playa Blanca (Schmitt, 1940; Manning, 1961; Manning and Reaka, 1979). Isla del Caño (Manning and Reaka, 1979).

RANGE.—East Pacific: known only from the two Costa Rican localities cited above.

HABITAT.—Sublittoral: 3–5 fms (5–9 m) (Schmitt, 1940; Manning, 1961); sand around base of pinnacle, 15 m (Manning and Reaka, 1979).

SIZE.—1♂ ca. 18 mm (Manning, 1961; Manning and Reaka, 1979); 2♀ 15–16.5 mm (Manning and Reaka, 1979).

COMMENTS.—This small species resembles *Nannosquilla decemspinosa* but occurs sublittorally rather than intertidally.

As pointed out by Manning and Reaka (1979: 639), one of the three specimens previously reported from off Costa Rica as *N. decemspinosa* proved to belong to this species; the other two specimens were correctly identified.

Discussion of Lysiosquillidae

Some lysiosquillids, especially Indo-West Pacific species of the genus *Lysiosquilla* Dana, have exceptionally broad geographic ranges. The larvae of lysiosquillids pass through a number of developmental stages (Alikunhi, 1967; Michel, 1970; see also Provenzano and Manning, 1978, for a list of species), and often settle at large sizes (see below), indicating extensive larval dispersal phases. Also, some lysiosquillids become larger than most other stomatopods.

Two related genera that occur in the East Pacific, *Lysiosquilla* and *Heterosquilla*, include species of very large (to 300 mm or more) and moderately large (to approximately 100 mm)

sizes, respectively. Two species of *Lysiosquilla, L. desaussurei* and *L. panamica,* occur along the mainland and the nearshore islands of the East Pacific. Also, in plankton samples off the Galapagos Islands, Michel (1970) found larvae of *Lysiosquilla* that differed from any of the species in the south central and western Pacific, indicating that an East Pacific species of *Lysiosquilla* also may occur on the offshore islands or that larvae have drifted that far offshore. *Lysiosquilla desaussurei* is more closely related to *L. hoevenii* (Herklots, 1851) in the East Atlantic than to the third species in this lineage, *L. scabricauda* (Lamarck, 1818), of the West Atlantic (Manning, 1977). *Lysiosquilla panamica* shows strongest affinities to *L. tredecimdentata* Holthuis, 1941, and related species in the Indo-West Pacific, and resembles to a lesser extent *L. glabriuscula* (Lamarck, 1818) and *L. campechiensis* Manning, 1962, in the West Atlantic (Manning, 1971a, 1972b). Postlarvae 19–34 mm in length have been reported for different species of *Lysiosquilla* (Alikunhi, 1967; Michel, 1970; Manning, 1969a, 1978a).

Three species of *Heterosquilla* occur in the East Pacific. A temperate species, *H. polydactyla,* occurs on the southern tip of South America, is closely related to *H. platensis* (Berg, 1900) in the Southwest Atlantic, and has more distant affinities to *H. tricarinata* Claus, 1871, in the Indo-West Pacific (Manning, 1969a). One fragment of a specimen of *H. insolita* has been reported from the Galapagos; this species also occurs in Florida, and is related to *H. insignis* (Kemp, 1911) in the Indo-West Pacific (Manning, 1969a). *Heterosquilla mccullochae,* reported in this study, inhabits one of the widest geographic ranges known for stomatopods (East Pacific, West Atlantic, Central Atlantic, and Indo-West Pacific; Manning 1969a, 1976b, 1977). Known postlarvae of *Heterosquilla* are 19–22 mm long (*H. polydactyla;* Manning, 1971b).

The remaining two East Pacific genera reported in this study, *Acanthosquilla* and *Nannosquilla,* are closely related and have moderately small body sizes (less than 70 mm and 45 mm, respectively; Manning, 1969a). Two amphi-American species of *Acanthosquilla* are known. *Acanthosquilla biminiensis* occurs in Pacific Central America and in widely scattered localities in the West Atlantic. This species is related to an East Atlantic and two Indo-West Pacific species, *A. septemspinosa* (Miers, 1881), *A. acanthocarpus* (Claus, 1871), and *A. multifasciata* (Wood-Mason, 1895), respectively (Manning, 1969a, 1977). Though uncommon, *A. digueti* also is reported both from the East Pacific and West Atlantic (Florida and Brazil; Manning, 1969a, 1974). Postlarvae of *Acanthosquilla* are moderately small (9–12 mm; Alikunhi, 1967; Camp, 1973; Manning, 1977).

In contrast to the above lysiosquillids, *Nannosquilla* is an exclusively American genus. All species are small and have relatively narrow ranges, and all of the East Pacific species are distinct from those in the West Atlantic. Eight species of *Nannosquilla* are known from the West Atlantic (Manning, 1969a, 1970, 1979). Including the species from this study, seven also are known from the East Pacific: *N. anomala* (southern California; Manning, 1967a), *N. californiensis* (Gulf of California and Costa Rica; Manning, 1961, this study), *N. decemspinosa* (Costa Rica, Panama, Colombia, and Peru; Manning, 1961, 1974), *N. canica* (Costa Rica; Manning and Reaka, 1979), *N. chilensis* (Chile; Dahl, 1954), and *N. galapagensis* and *N. similis* (Galapagos; Manning, 1972b). *Nannosquilla galapagensis* and *N. similis* resemble other East Pacific species (*N. decemspinosa, N. chilensis,* respectively; Manning, 1972b).

In addition, two other genera of relatively small body size occur in the East Pacific but were not recorded in the present study. Two East Pacific species of *Coronida, C. schmitti* and *C. glasselli,* closely resemble an East Atlantic congener, *C. bradyi* (Manning, 1976a, 1977). The genus is not represented in the West Atlantic or the Indo-West Pacific. A small related lysiosquillid known only from Cocos Island, *Neocoronida cocosiana,* provides one of the closest links between the East Pacific and Indo-West Pacific stomatopod fauna. This species closely resembles *N. trachurus* (von Martens, 1881), one of the two other species in the

genus, both of which occur in the Indo-West Pacific region (Manning, 1972b, 1976a, 1978b).

Lysiosquillids generally dig vertical burrows in sandy environments. Some species of *Nannosquilla* attach free eggs (approximately 0.8 mm in diameter) to the mucoid and sand lining of the burrow (Manning, 1979), in contrast to the gonodactylids, squillids, and pseudosquillids, all of which carry the compact egg mass in their maxillipeds. In this study, lysiosquillids were collected burrowing in sand in the same rock and rubble strewn sites with *Gonodactylus* and *Meiosquilla.* The lysiosquillids appeared to occur in relatively low densities, and exhibited defensive but little offensive fighting behavior, compared to the aggressive gonodactylids (M.L.R., personal observation).

Family Pseudosquillidae Manning, 1977

Parasquilla similis Manning, 1970

Parasquilla (Parasquilla) similis Manning, 1970:144, fig. 9.—Del Solar et al., 1970:37.

Material.—Near Isla del Caño: Sta 485, 73 m: 1♂ 117 mm.

Previous Costa Rican Records.—None.

Range.—East Pacific: Isla del Caño, Costa Rica, 08°46′35″N, 83°54′W, to Caleta la Cruz, 03°38′S, near Tumbes, Peru [03°34′S, 80°28′W]. Mainland and nearshore islands.

Habitat.—Sublittoral, deep shelf and upper slope; 84 m (Manning, 1970); 125 m (Del Solar et al., 1970); mud, 73 m (this study).

Size.—3♂ 151–160 mm, 3♀ 125–135 mm (Manning, 1970); 1♂ 117 mm (this study).

Comments.—This relatively large, deep-dwelling species has been collected previously only from the Gulf of Panama and Peru.

Pseudosquillopsis marmorata (Lockington, 1877)

Pseudosquilla marmorata Lockington, 1877:33.
Pseudosquillopsis marmorata.—Manning, 1969b:527, 531, figs. 1, 3; 1972a:106.

Material.—Near Isla del Caño: Sta 485, 73 m: 1♂ 120 mm.

Previous Costa Rican Records.—None.

Range.—East Pacific: San Diego, California [32°42′N, 122°50′W] to the Galapagos Islands [00°30′S, 90°30′W]. Mainland from San Diego to Costa Rica, including the Gulf of California, nearshore islands [Isla La Plata, Ecuador, 01°-16′S, 81°06′W], and offshore islands.

Habitat.—Littoral and sublittoral; low tide, on sandy mud flats (Lockington, 1877); night light (postlarva) and sand, shale, rock, 81–99 m (Manning, 1969b); 64 m (postlarva; Manning, 1972a); mud, 73 m (this study).

Size.—96.5 mm (Lockington, 1877); 3♂ postlarvae 25–28 mm, 8♀ postlarvae 25–28 mm, 1♀ juv 40 mm (Manning, 1969b); 1♂ postlarva 28 mm (Manning, 1972a); 1♂ 120 mm (this study). Overall size of males 25 to 120 mm, of females 25 to 40 mm.

Comments.—Postlarvae of *Pseudosquillopsis marmorata* settle at relatively large sizes (25–28 mm) and grow to a relatively large size (120 mm) as adults. They occupy diverse substrates over a broad depth range (0–99 m).

On the South American mainland, *P. marmorata* is replaced by the closely related *P. lessonii.*

Discussion of Pseudosquillidae

Only one East Pacific species of *Parasquilla,* related to three West Atlantic and one East Atlantic species, has been recorded. Two Indo-West Pacific species, in a related genus, *Faughnia,* are known; until recently the older of the two was considered to belong to the genus *Parasquilla* (Manning and Makarov, 1978). All of these species occur in relatively deep, frequently muddy environments (Manning, 1969a, 1970, 1977).

Pseudosquillopsis, on the other hand, is represented by two species in the East Pacific, *P. marmorata* and *P. lessonii*; no species in the West Atlantic; and one species each in the East Atlantic and Indo-West Pacific (Manning, 1969b, 1972a, 1977). Little is known of the habits of these uncommonly collected species, but they apparently occupy diverse substrates over a broad depth range. Larval periods appear to be ex-

tended. In addition to the postlarvae (25–28 mm) and juvenile (40 mm) reported for *P. marmorata,* postlarvae 30–33 mm of *P. lessonii* and of *P. cerisii* (Roux, 1828) (East Atlantic) are known (Manning, 1969b, 1977).

An endemic species of another genus in this family, *Pseudosquilla adiastalta,* occurs along the mainland, from Mexico to Ecuador, and on the Tres Marias, Cocos (USNM), Clarion, Clipperton, and Galapagos islands in the East Pacific (Manning, 1964, 1972a, 1972d, 1976a). This species is most closely related to Indo-West Pacific species [*P. oculata* (Brullé, 1837), *P. guttata* Manning, 1972; Manning, 1964, 1972d]. Seven widespread species of *Pseudosquilla* occur in the Indo-West Pacific. Two of these, *P. ciliata* (Fabricius, 1787) and *P. oculata,* also occur in the East and West Atlantic. *Pseudosquilla ciliata* has unusually many, small eggs (Reaka, 1979). The postlarvae of *P. ciliata* range from 17.5–19 mm (Manning, 1968, 1969a, 1977); those of *P. oculata* are 24–30 mm (Manning, 1969a, 1977), and those from *P. guttata* are 25 mm long (Manning, 1972d). Postlarvae of *Hemisquilla ensigera,* another pseudosquillid known from East Pacific waters, but not reported in this study, are 29.5 mm in length (Manning, 1972c). These observations, together with those on the postlarvae of *Pseudosquillopsis,* suggest that the larvae of pseudosquillids may spend long periods in the plankton.

Family SQUILLIDAE Latreille, 1803

Cloridopsis dubia (H. Milne Edwards, 1837)

Squilla dubia.—Schmitt, 1940:155, fig. 7.

Cloridopsis dubia.—Manning, 1969a:141, figs. 39b, 41.—Del Solar et al., 1970:36—Manning, 1974:107, fig. 3.

MATERIAL.—NEAR ISLA DEL CAÑO: Sta 485, 73 m: 1♀ 65 mm.

PREVIOUS COSTA RICAN RECORDS.—Puntarenas (Schmitt, 1940).

RANGE.—American. East Pacific: from El Triunfo, El Salvador [13°17′N, 88°33′W] to Rio Tumbes, Peru [Tumbes, 03°34′S, 80°28′W]. West Atlantic: from South Carolina to Brazil. Mainland.

HABITAT.—Littoral and sublittoral. East Pacific: salt lake; low tide at entrance of Panama Canal (Schmitt, 1940); 9 m; mouth of river (Manning, 1974); mud, 73 m (this study).

SIZE.—East Pacific: 5♂ 35–126 mm, 3♀ 120–147 mm (Manning 1974); 1♀ 65 mm (this study). West Atlantic: 40♂ 49.5–155.5 mm, 15♀ 87–142 mm. Overall size range of males 35 to 155.5 mm, of females 65 to 147 mm.

COMMENTS.—*Cloridopsis dubia* generally occurs on shallow mud flats on both coasts of the Americas, but was taken from a relatively deep site here. This is a comparatively large species, adults attaining a length of 150 mm or more. Some morphological differences have been noted between East Pacific and West Atlantic populations (Manning, 1969a:145).

Meiosquilla dawsoni Manning, 1970

Meiosquilla dawsoni Manning, 1970:102, fig. 3; 1972a:102; 1974:108.

MATERIAL.—PUERTO JIMINEZ: Sta 497, intertidal: 3♀ 28–34 mm.

PREVIOUS COSTA RICAN RECORDS.—Puerto Culebra (Manning, 1972a).

RANGE.—East Pacific: Guaymas, Mexico [27°-56′N, 110°54′W] to Balboa, Panama [08°57′N, 79°34′W]. Mainland shore.

HABITAT.—Intertidal and shallow sublittoral, including: among rocks in sand pool, 0.1 m (Manning, 1970); sandy mud, 25.5 m (Manning, 1972a); stream in intertidal mud flat (this study).

SIZE.—2♂ 29.5–47 mm (Manning, 1970); 1♂ 19mm (Manning, 1972a); 1♂ 28 mm, 1♀ 29 mm (Manning, 1974); 3♀ 28–34 mm (this study). Overall size of males 19 to 47 mm, of females 28 to 34 mm.

COMMENTS.—This uncommonly collected species occurs on a wide range of substrate types (including sand, mud, or among rocks) over a moderate depth range (0 to 25 m) and can tolerate low salinities, as indicated by its occurrence in a stream in Costa Rica. Few if any stomatopods have invaded exclusively fresh-water habitats, although some squillids and lysiosquillids occur in

estuarine conditions (examples in Manning 1969a, 1974, 1977). *Meiosquilla dawsoni* reaches a larger size (47 mm) than either *M. oculinova* or *M. swetti.*

Meiosquilla oculinova (Glassell, 1942)

Squilla oculinova Glassell, 1942:53, fig. 7.
Meiosquilla oculinova.—Manning, 1972a:101; 1976a:223.

MATERIAL.—BAHIA HERRADURA: Sta 450, 17 m: 6♂ 19–26 mm, 4♀ 19–29 mm. ISLA SALERA: Sta 464, 17 m: 4♂ 14–23 mm, 2♀ 15–21 mm, 2 juvs 13–14 mm. ISLA DEL CAÑO: Sta 471, 9 m: 5♂ 14.5–24.5 mm, 9♀ 19–30 mm; Sta 472, 15 m: 1♂ 16 mm, 1♀ 22 mm; –, intertidal: 1♀ 30 mm; Sta 487, 9 m: 4♂ 22–31 mm, 6♀ 27–31 mm; Sta 491, 20 m: 8♂ 14.5–30 mm, 6♀ 17–26 mm; –,10–15 m: 1♂ 23 mm, 1♀ 30 mm.

PREVIOUS COSTA RICAN RECORDS.—None.

RANGE.—East Pacific: Bahía Chamela, Mexico [19°33′N, 105°07′W] to Isla La Plata, Equador, 01°15.5′S, 81°05′W. Mainland and nearshore islands.

HABITAT.—Shallow sublittoral, including: 18–23 m (Glassell, 1942); bedrock, boulders, gravel, sand, 6.1–9.2 m; rocks with crevices, 3.7–18.3 m; hard bedrock, boulders, rubble, 0–4.6 m; coral, silt, sand, 9.2–27.6 m (Manning, 1976b); mud, shell, rocks, sand; rocks; sand, rocks and coral rubble; coral rubble; 0–20 m (this study).

SIZE.—1♀ 36 mm (Glassell, 1942); 4♂ 9–31 mm, 6♀ 14–33 mm (Manning, 1976a); 29♂ 14–31 mm, 30♀ 15–31 mm, 2 juvs 13–14 (this study). Overall size range of males 9 to 31 mm, of females 14 to 36 mm.

COMMENTS.—Although this species has been recorded previously only from a few widely scattered localities (Manning, 1972a, 1976b), *Meiosquilla oculinova* was the most common species in number of localities and individuals recorded in this study. A small species less than 40 mm long, *M. oculinova* occupies a variety of habitats (usually holes in and under rock, shell, or coral rubble) from intertidal areas (not common) to about 30 m. These small brown squillids are lightly striped across the abdominal segments, but lack bright coloration or meral spots. Observations showed that they defend hiding sites in crevices and attack other individuals that approach them. The raptorial appendages are lowered and spread parallel to the body, giving the animal a "sled-like" appearance, and the strikes are less potent and less frequent than those delivered by gonodactylids. Despite its less aggressive mien, *M. oculinova* frequently was collected at the same site with various gonodactylids (particularly *Gonodactylus zacae* and *G. bahiahondensis*). Although individuals of *Meiosquilla* were more numerous in rocky habitats than gonodactylids, and the converse was true in coral rubble, neither *Meiosquilla* nor the gonodactylids appeared to exclude the other from rocks and rubble at the same site.

Meiosquilla swetti (Schmitt, 1940)

Squilla swetti Schmitt, 1940:146, fig. 3.
Meiosquilla swetti.—Manning, 1972a:102; 1974:108.

MATERIAL.—NEAR PUNTA QUEPOS: Sta 462, 21 m: 1♂ 42 mm. ISLA DEL CAÑO: Sta 472, 15 m: 1♂ 27 mm; Sta 487, 9 m: 1♀ 33 mm.

PREVIOUS COSTA RICAN RECORDS.—None.

RANGE.—East Pacific: Bahía de Petatlán, Mexico [17°34′N, 101°30′W] to Isla Taboguilla, Panama [08°48′N, 79°31′W]. Mainland and nearshore islands.

HABITAT.—Shallow sublittoral, including: 45 m (Schmitt, 1940); mud, 29–42 m; mangrove leaves, 3 m (Manning, 1972a); sand, 5.4 m (Manning, 1974); sand, rocks and coral rubble; coral rubble; 9–21 m (this study).

SIZE.—1♀ 28 mm (Schmitt, 1940); 1♂ 19 mm, 1♀ 31 mm (Manning, 1972a); 1♀ 30 mm (Manning, 1974); 2♂ 27–42 mm, 1♀ 33 mm (this study). Overall size range of males 19 to 42 mm, of females 28 to 33 mm.

COMMENTS.—This infrequently recorded but relatively broad ranging species had been taken previously only in muddy environments, but this study shows that *Meiosquilla swetti* also occurs in rubble habitats. Thus, *M. swetti* appears to occupy a broader range of habitats with a greater depth range (0–45 m) than *M. oculinova. Meiosquilla swetti* also attains somewhat larger sizes (42 mm) than *M. oculinova.*

Squilla aculeata aculeata Bigelow, 1893

Chloridella aculeata.—Lunz, 1937:8.

Squilla aculeata.—Bigelow, 1894:523, figs. 15, 16.—Schmitt, 1940:158, fig. 9.—Bahamonde, 1968:116.—Del Solar et al., 1970:36.

Squilla aculeata aculeata.—Manning, 1972a:102; 1974:108.

MATERIAL.—NEAR ISLA DEL CAÑO: Sta 485, 73 m: 1♂ 57 mm.

PREVIOUS COSTA RICAN RECORDS.—None.

RANGE.—East Pacific: .Teacapán, Mexico [22°33′N, 105°45′W] to Iquique, Chile [20°13′S, 70°10′W] (Bahamonde, 1968). Mainland and nearshore islands. Another subspecies, *Squilla aculeata calmani* Holthuis, 1959, occurs in the East Atlantic (Manning, 1977).

HABITAT.—Intertidal and sublittoral, including: tide pools (Schmitt, 1940); mud, 9.1 and 12.8 m (Manning, 1972a); mud, 73 m (this study).

SIZE.—1♂ 150 mm, 1♀ 68.5 mm (Bigelow, 1894); 1♀ 197 mm (Lunz, 1937); 1♂ 68 mm, 8♀ 36–110 mm (Schmitt, 1940); 1♂ 65 mm, 2♀ 35–82 mm (Manning, 1972a); 1♂ 157 mm (Manning, 1974); 1♂ 57 mm (this study). Overall size range of males 57 to 157 mm, of females 35 to 197 mm. Adults of *Squilla aculeata calmani* attain a similar size, 150 mm (Manning, 1977).

COMMENTS.—This mud-dwelling species has a moderate depth range (0 to 73 m) and reaches relatively large sizes in the East Pacific. In the East Atlantic, *S. a. calmani* is of similar size and has been recorded from diverse muddy and sandy habitats at depths ranging from 0 to 44 m; it also occurs in or near the mouths of rivers (Manning, 1977).

Squilla hancocki Schmitt, 1940

Squilla hancocki Schmitt, 1940:160, fig. 10.—Manning, 1972a:102; 1972c:303.—Del Solar 1972:17.—Manning, 1976a:223.

MATERIAL.—GOLFO DUCE: Sta 500, 55 m: 4♂ 38–49 mm, 3♀ 47–54 mm.

PREVIOUS COSTA RICAN RECORDS.—None.

RANGE.—East Pacific: Bahía de Petatlán, Mexico [17°34′N, 101°30′W] to Paita, Peru [05°06′S, 81°07′W]. Mainland and nearshore islands.

HABITAT.—Sublittoral, including: 45 m; 27–36 m; muck bottom, 36 m (Schmitt, 1940); sandy mud, 54–73 m; mud, 29–42 m; mud, 55 m (Manning, 1972a); 220 m (Peru; Manning, 1972c; Del Solar, 1972); 91.5 m (Colombia; Manning, 1976a); mud, 55 m (this study).

SIZE.—4♀ to 60 mm (Schmitt, 1940); 5♂ 20–68 mm, 7♀ 32–64 mm (Manning, 1972a); 1♂ 61 mm (Manning, 1972c); 1♂ 42 mm (Manning, 1976a); 4♂ 38–49 mm, 3♀ 47–54 mm (this study). Overall size of males 20 to 68 mm, of females 32 to 64 mm.

COMMENTS.—This moderately small (total length less than 70 mm), relatively rare East Pacific squillid occupies deep (27 to 220 m) muddy environments.

Squilla panamensis Bigelow, 1891

Squilla panamensis.—Bigelow, 1894:526, figs. 17, 18 [part].—Schmitt, 1940:166, fig. 13.—Del Solar et al., 1970:36.—Manning, 1972a:103; 1974:108.

MATERIAL.—BAHÍA HERRADURA: Sta 455, 55 m: 1♂ 33 mm. GOLFO DULCE: Sta 500, 55 m: 10♂ 32–73 mm, 11♀ 53–115 mm.

PREVIOUS COSTA RICAN RECORDS.—Bahía Ballena, Golfo de Nicoya (2 stations; Manning, 1972a).

RANGE.—East Pacific: off Mazatlan, Mexico, 23°12′N, 106°40′W, to Tumbes, Peru [03°34′S, 80°28′W]. Mainland and nearshore islands.

HABITAT.—Sublittoral, on muddy bottoms, including: 48–86 m (Bigelow, 1894); 45 m; green mud, 46.8–84.6 m; and mud, 18 m (Schmitt, 1940); 20–70 m (Del Solar et al., 1970); 102 m; sandy mud, 54–73 m; mud, 63.7–73 m; mud, 63.7 m; sandy mud, 64 m (Manning, 1972a); mud, 55 m (this study).

SIZE.—140 mm (Bigelow, 1894); 8♂ 58–101 mm, 5♀ 52–95 mm (Manning, 1972a); 1♀ 74 mm (Manning, 1974); 10♂ 32–73 mm, 11♀ 53–115 mm (this study). Overall size of males 32 to 101 mm, of females 52 to 115 mm.

COMMENTS.—*Squilla panamensis* is considerably larger than *S. hancocki*, attaining a total length of at least 140 mm, and occupies muddy environ-

ments in moderately deep water (18 to 102 m). Like *S. hancocki,* it is restricted to the East Pacific.

Discussion of Squillidae

The genus *Meiosquilla* occurs in the East Atlantic and off South Africa (five species), West Atlantic (five species), and the East Pacific (three species) (Manning, 1969a, 1972a, 1977). All species are relatively small, usually less than 40 mm long (although *M. swetti*, *M. dawsoni*, and two East Atlantic species exceed that size). Morphological differences differentiate East Atlantic species (claw with 5 teeth) from their American congeners (claw with 4 teeth). The East Pacific *M. dawsoni* resembles the West Atlantic *M. quadridens* (Bigelow, 1893), and *M. swetti* resembles *M. schmitti* (Lemos de Castro, 1955) and *M. randalli* (Manning, 1962) from the West Atlantic (Manning, 1970). The other East Pacific species, *M. oculinova*, lacks close ties with West Atlantic species. It is unique among stomatopods in possessing geniculate spines on the antennular peduncle and anteriorly scalloped margins (the functions of which are unknown) on the eyes (Glassell, 1942: fig. 7).

The small size of American *Meiosquilla* may be associated with living in crevices among rocks (note that East Atlantic species may be level-bottom forms and thus differ from American species in habitat; see Lewinsohn and Manning, 1980:9), and their size, like some of their morphological features, may reflect a neotenic origin (Manning, 1969a:103). As seen in this study, off Costa Rica *Meiosquilla* occupies coarse habitats of rock and rubble, and associates more frequently with various gonodactylids than with other squillids. Postlarvae of *Meiosquilla*, known from two West Atlantic species, settle at 12–13 mm in length (Manning, 1969a).

Members of the genus *Squilla* are found in the East Atlantic (three species), West Atlantic (19 species), and East Pacific (eight species). *Squilla aculeata*, the only species of the genus with populations in more than one of the three regions, is represented by subspecies in the East Pacific and East Atlantic; in the West Atlantic this species is replaced by a relative, *S. empusa* Say, 1818 (Manning, 1969a, 1977). *Squilla biformis* in the East Pacific is specifically distinct from but closely related to *S. intermedia* Bigelow, 1893, in the West Atlantic and to *S. cadenati* Manning, 1970, in the East Atlantic (Manning, 1969a, 1977). Three other pairs of cognates also occur in the East Pacific and West Atlantic, respectively: *S. panamensis–S. brasiliensis* Calman, 1917; *S. tiburonensis–S. lijdingi* Holthuis, 1959; and *S. hancocki–S. deceptrix* Manning, 1969 (Manning, 1969a).

Although one amphi-American species of *Cloridopsis* is known, the genus otherwise occurs in the Indo-West Pacific region (Manning, 1969a). Two species of *Schmittius*, an East Pacific genus not known to occur in Costa Rican waters, are most closely related to an Indo-West Pacific genus, *Squilloides* (Manning, 1972b, 1977). Also, one squillid, *Clorida mauiana*, occurs off Baja California as well as Hawaii and the Santa Cruz Islands in the Indo-West Pacific, providing the second instance (in addition to *Heterosquilla mccullochae*) of one species of stomatopod that occurs both in the East Pacific and the Indo-West Pacific (Manning, 1976b).

Habitat and Associations

The tabulation of species occurrences in major habitats, given below (Table 2), indicates that coral rubble, frequently in association with rocks, was the dominant habitat populated by the Gonodactylidae. Most of the gonodactylids occurred in exclusively rocks and/or coral rubble habitats. Several lysiosquillids also were found in coral rubble habitats, although they dig burrows in the coral sand substrate there (see Station List, Table 1, above). *Acanthosquilla* also was found in sand where coral was not present. Lysiosquillids generally did not occupy rocky habitats. As a family, the squillids occupied a broad range of habitats. Some species, however, including *Meiosquilla oculinova* and *M. swetti*, were found in rock and coral rubble habitats, in this respect resembling gonodactylids. These species lived in crevices among

TABLE 2.—Number of individuals collected from major habitat types (many sites in which coral rubble was the dominant habitat characteristic also contained rocks and pockets of sand; asterisk (*) by samples from sand indicate that rocks also were present nearby; PL = postlarvae; juvs = juveniles)

Species	*Mud*	*Sand*	*Rock-shell*	*Coral rubble*
GONODACTYLIDAE				
Gonodactylus albicinctus			2	1
G. bahiahondensis			4	24
G. costaricensis			3	5
G. festae				15
G. stanschi			2	4
G. zacae			1	26
gonodactylid PL-juvs			3	3
Total	0	0	15	78
LYSIOSQUILLIDAE				
Heterosquilla mccullochae		2*		4
Nannosquilla californiensis				6
N. canica		2*		
Acanthosquilla biminiensis		2, 1*		
Lysiosquilla desaussurei		(surface, 1)		
Total	0	7	0	10
SQUILLIDAE				
Meiosquilla oculinova			32	29
M. swetti				3
M. dawsoni	3			
Squilla aculeata	1			
S. hancocki	7			
S. panamensis	22			
Cloridopsis dubia	1			
squillid PL-juvs	5		2	1
Total	39	0	34	33
PSEUDOSQUILLIDAE				
Pseudosquillopsis marmorata	1			
Parasquilla similis	1			
Total	2	0	0	0
Total individuals	41	7	49	121
Total localities collected	6	2	4	7

and under rocks, rather than in holes in coral. Other squillids, including *M. dawsoni*, occupied muddy habitats exclusively. The pseudosquillids (including representatives of *Parasquilla* and *Pseudosquillopsis*, but not *Pseudosquilla*!) were collected also only in muddy environments.

Overall, when compared to the number of collections made in each type of habitat, stomatopods were recorded most frequently from coral rubble habitats. Of 20 species collected, 12 occurred in coral rubble or rock (or sand associated with rubble and rock), seven in mud, and one in sand without rubble. Within the rock-rubble environment, different species occupied different micro-habitats. Numbers of individuals in *Gonodactylus* were higher in predominantly coral rubble (78) than rock-shell (15) habitats; individuals of *Meiosquilla oculinova* occurred equally frequently in coral rubble (32) and rock-shell (29) habitats (though collections were made in seven and four localities of these habitats, respectively); thus, *Meiosquilla* was more strongly associated with

rocky environments than was *Gonodactylus*. Lysiosquillids used the sandy substrate of these rock and rubble habitats.

The number of times different species were collected at different depths is shown in Table 3. Like the gonodactylids, the lysioquillids and *Meiosquilla* occurred in relatively shallow depths, but mud-dwelling squillids (except *M. dawsoni*) and pseudosquillids were found only in relatively deep water. Fourteen species were collected in habitats shallower than 25 m, six species occurred exclusively in deeper water.

During the study, 218 stomatopods were collected at 19 localities. *Meiosquilla oculinova* was the most common species, occurring in eight (42%) of these sites (61 individuals = 28% of total collected); it occupied eight of 11 sites (73%) with rocks and coral rubble, and eight of 13 sites (62%) with depths between 0 and 25 m. *Gonodactylus bahiahondensis* and *G. zacae* each were collected from seven localities (34% of total sites, 64% of rock and coral rubble sites, 54% of sites with depths between 0 and 25 m; 28 and 27 individuals = 14% and 13% of total). *Gonodactylus stanschi*, *G. costaricensis*, *Heterosquilla mccullochae*, and *Meiosquilla swetti* each occurred in 3–4 sites (16%–21% of total sites, 27%–36% of sites with rock and rubble, 23%–31% of sites shallower than 25 m),

TABLE 3.—Number of individuals collected at different depths (m)

Species	*0–1*	*2–10*	*11–25*	*26–50*	*51–75*
GONODACTYLIDAE					
Gonodactylus albicinctus		1	2		
G. bahiahondensis	20	2	6		
G. costaricensis	4	1	3		
G. festae	15				
G. stanschi	3	1	2		
G. zacae	6	13	7	1	
Gonodactylid PL-juvs	2		4		
Total	50	18	24	1	0
LYSIOSQUILLIDAE					
Heterosquilla mccullochae		1	5		
Nannosquilla californiensis		6			
N. canica			2		
Acanthosquilla biminiensis			3		
Lysiosquilla desaussurei	(swimming, 1)				
Total	—	7	10	0	0
SQUILLIDAE					
Meiosquilla oculinova	1	24	36		
M. swetti		1	2		
M. dawsoni	3				
Squilla aculeata					1
S. hancocki					7
S. panamensis					22
Cloridopsis dubia					1
Squillid PL-juvs			3	2	3
Total	4	25	41	2	34
PSEUDOSQUILLIDAE					
Pseudosquillopsis marmorata					1
Parasquilla similis					1
Total	0	0	0	0	2
Total individuals	54	50	75	3	36
Total localities collected	3	2	8	2	4

but large numbers of individuals were not found (3%, 4%, 3%, and 1% of total numbers of individuals, respectively). *Gonodactylus festae* occurred at only one intertidal site but was the fourth most common species in number of individuals (15 = 17% of total number of individuals).

Postlarval (PL) and juvenile gonodactylids were collected among rocks and coral rubble at depths between 0 and 17 m. *Gonodactylus* postlarvae or juveniles were found with adults of the genera *Gonodactylus*, *Meiosquilla*, *Heterosquilla*, *Acanthosquilla*, and *Nannosquilla* at Isla del Canõ, but in one locality (Isla Salera, station 464) only small *Gonodactylus* were found. Squillid larvae and postlarvae were collected alone at 37 and 62 m on mud (stations 451, 484); in mud, shell, and rocks at 20 m with *Gonodactylus* (station 447); and in rock, sand, and coral rubble at 10–15 m with members of *Gonodactylus*, *Meiosquilla*, and *Heterosquilla* (Isla del Caño). The only juveniles of *Meiosquilla* taken occurred with their adults (station 464). These results suggest that juvenile *Gonodactylus* generally settle in habitats typically occupied by adults, though in one locality no adults were obtained. The juveniles of squillids occupied more diverse habitats.

As shown in Table 1, species were collected more frequently in association with several others than alone. The highest numbers of co-occurring species were recorded in coral rubble and rock habitats (gonodactylids, most lysiosquillids, *Meiosquilla*); as many as eight of the 12 species recorded from these habitats occurred together. In general, however, the number of species found together at one site varied considerably, indicating relatively loose associations between given species.

The frequency with which particular species co-occurred with others in different localities is summarized in tabular form here (Table 4). Strong overlap occurred among the gonodactylids, most lysiosquillids, and *Meiosquilla*. The mud-dwelling species showed similar patterns of association. Species were likely to occur with any of the other species in their habitat type, and the species recorded from the most sites (*Meiosquilla oculinova*, *Gonodactylus bahiahondensis*, *G. zacae*) occurred together most frequently. When numbers of individuals co-occurring with other species are considered, the same trends are apparent (these data are available upon request). These results suggest that species co-occurrence is controlled more by general habitat type and abundance than by preferential associations among particular species.

Zoogeographical Relationships of East Pacific Stomatopoda

The East Pacific stomatopod fauna demonstrates a high degree of endemism, even though these crustaceans produce pelagic larvae that spend from several weeks to several months in the plankton (Alikunhi, 1967; Michel, 1970; Pyne, 1972; Provenzano and Manning, 1978). All eight species of the family Gonodactylidae are endemic to the East Pacific. Of the lysiosquillids, both species of *Lysiosquilla*, all seven species of *Nannosquilla*, both species of *Coronida*, and the single species of *Neocoronida* occur only in the East Pacific region. However, two species of *Heterosquilla* (*H. insolita* and a south temperate species, *H. polydactyla*) also occur in the West Atlantic, and one species (*H. mccullochae*) is circumtropical. The two species of *Acanthosquilla* (*A. biminiensis*, *A. digueti*) occur both in the East Pacific and the West Atlantic. Of the squillids, all three species of *Meiosquilla* are endemic to the East Pacific, as are the two species of the endemic genus *Schmittius* and seven species of *Squilla*. *Cloridopsis dubia*, however, is found in both the East Pacific and the West Atlantic; one species of *Squilla*, *S. aculeata*, is represented by subspecies in the East Pacific and East Atlantic; and *Clorida mauiana* occurs in the East Pacific, Hawaii, and the Santa Cruz Islands in the Indo-West Pacific. Subspecies of another squillid, *Pterygosquilla armata*, occur in temperate waters in Argentina and Chile, New Zealand, and South Africa (Manning, 1969c). Of the pseudosquillids, one species of *Parasquilla*, two species of *Pseudosquillopsis*, and one species of *Pseudosquilla* are known only from the East Pacific, but sub-

TABLE 4.—Frequencies with which species co-occur in different localities (numbers in boxheads refer to species in left column; N = no other species)

Species	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*	*18*	*19*	*20*	*21*	*22*	*N*
GONODACTYLIDAE																							
1. *Gonodactylus bahiahondensis*		1	3	5	4	1	3	3	1	1	1		6	1						1			
2. *G. festae*	1		1	1	1		1						1										
3. *G. stanschi*	3	1		2	2	1	2	1	1				3										
4. *G. zacae*	5	1	2		3	1	2	3	1	1	1		6	2						1			1
5. *G. costaricensis*	4	1	2	3		1	1	1	1				3										
6. *G. albicinctus*	1		1	1	1			1	1				2							1			
7. PL-juvs	3	1	2	2	1			1		1	1		3	1									
LYSIOSQUILLIDAE																							
8. *Heterosquilla mccullochae*	3		1	3	1	1	1		1	1	1		3	2						1			
9. *Nannosquilla californiensis*	1		1	1	1	1		1					1										
10. *N. canica*	1			1			1	1			1		1	1									
11. *Acanthosquilla biminiensis*	1			1			1	1		1			1	1									1
12. *Lysiosquilla desaussurei*																							1
SQUILLIDAE																							
13. *Meiosquilla oculinova*	6	1	3	6	3	2	3	3	1	1	1			2						2			
14. *M. swetti*	1			2			1	2		1	1		2										
15. *M. dawsoni*																							1
16. *Squilla aculeata*																			1		1	1	
17. *S. hancocki*																		1					
18. *S. panamensis*																	1						1
19. *Cloridopsis dubia*																1					1	1	
20. PL-juvs	1			1		1		1					2							2			2
PSEUDOSQUILLIDAE																							
21. *Pseudosquillopsis marmorata*																1			1			1	
22. *Parasquilla similis*																1			1		1		

species of *Hemisquilla ensigera* occur in the northeast Pacific (southern California, Mexico, and Panama), the southeast Pacific (Chile), and off eastern Australia (Manning, 1972a, 1972c, 1974). Two species of *Eurysquilla* (Eurysquillidae) are endemic to the East Pacific, and the genus occurs also in the East and West Atlantic and in the Indo-West Pacific (Manning, 1970, 1972a, 1977). Overall, 38 of the 50 East Pacific species (76%) are specifically distinct from relatives elsewhere, and 10 species (0/8 gonodactylids, 5/17 lysiosquillids, 4/17 squillids, 1/6 pseudosquillids, 0/2 eurysquillids) occur outside of the confines of the East Pacific region. However, among the 45 tropical and subtropical East Pacific stomatopods, only seven species (16%) (0/8 gonodactylids, 4/16 lysiosquillids, 3/15 squillids, 0/4 pseudosquillids, 0/2 eurysquillids) are shared with other regions.

Several species in the East Pacific are shared with the West Atlantic (*Heterosquilla mccullochae*, *H. polydactyla*, *H. insolita*, *Acanthosquilla biminiensis*, *A. digueti*, *Cloridopsis dubia*, and *Pterygosquilla armata*). Two of these (*Heterosquilla polydactyla*,

Pterygosquilla armata) are south temperate species connected to the West Atlantic via Cape Horn, and *Heterosquilla mccullochae* is circumtropical. The record of *Heterosquilla insolita* in the Galapagos Islands is based upon a damaged specimen; if it is not conspecific, it is unquestionably closely related to the West Atlantic species (Manning, 1969a). Therefore, five (ca. 11%) of the 45 warm-water species of the East Pacific also occur in the West Atlantic. In addition, many species endemic to the East Pacific (e.g., representatives of *Gonodactylus*, *Nannosquilla*, *Meiosquilla*, *Squilla*) show close affinities to West Atlantic species. Including shared and closely related species, 60% of the East Pacific species have closest affinities to West Atlantic species.

Several taxa, including *Coronis* and *Platysquilla* (Lysiosquillidae), are represented by species in the West Atlantic but not in the East Pacific (Manning, 1969a, 1977). Two species, *Bathysquilla microps* (Manning, 1961) (Bathysquillidae) and *Odontodactylus brevirostris* (Miers, 1884) (Gonodactylidae), inhabit the West Atlantic and Indo-West Pacific (both have been taken off Hawaii) but not the East Pacific (Manning, 1969a; Manning and Struhsaker, 1976) or the East Atlantic (Manning, 1977).

Five (ca. 11%) tropical East Pacific species either resemble East Atlantic more than they do West Atlantic relatives, or a West Atlantic cognate is absent (*): *Squilla aculeata aculeata–S. aculeata calmani*; *Lysiosquilla desaussurei–L. hoevenii*; *Coronida glasselli–C. bradyi* (*); *Pseudosquillopsis lessonii–P. cerisii* (*); *Eurysquilla solari–E. galatheae* Manning, 1977 and *E. leloeuffi* Manning, 1977 (Manning, 1977).

In contrast to the Atlantic affinities discussed above, two species (*Heterosquilla mccullochae* and *Clorida mauiana*) occur in both the East Pacific and the Indo-West Pacific, and several other East Pacific taxa show strong Indo-West Pacific affinities: *Lysiosquilla panamica–L. tredecimdentata*; *Neocoronida cocosiana–N. trachurus*; *Pseudosquilla adiastalta–P. oculata* and *P. guttata*; *Schmittius peruvianus* and *S. politus–Squilloides* spp. Therefore, about 16% of the warm-water stomatopods from the East Pacific have closest affinities to Indo-West Pacific taxa. Also, two cold-water species in the East Pacific (*Hemisquilla ensigera* and *Pterygosquilla armata*) are represented by different subspecies in Indo-West Pacific localities (Manning, 1977). Moderate body sizes and long larval lives characterize many of these genera. Dispersal may account for the Indo-West Pacific elements in the East Pacific stomatopod fauna; however, some species cross the central Pacific expanse and reach only the offshore islands of the East Pacific.

All of the species of stomatopods reported in the present collections, and most of those from the East Pacific, occur along the mainland and nearshore islands. Of 50 East Pacific species, only nine have been recorded from the more remote offshore islands: *Gonodactylus zacae*, *G. pumilus*, *Nannosquilla galapagensis*, *N. similis*, *Coronida schmitti*, *Neocoronida cocosiana*, *Heterosquilla insolita*, *Pseudosquillopsis marmorata*, and *Pseudosquilla adiastalta* (Manning, 1969a, 1970, 1972a,b, 1976a); this does not include the larva of *Lysiosquilla* sp. reported from the Galapagos by Michel (1970). Eight of the nine occur in the Galapagos Islands. Three species (*Gonodactylus pumilus*, *Nannosquilla galapagensis*, *N. similis*) are endemic to the Galapagos Islands, and one (*Neocoronida cocosiana*) occurs only off Cocos Island. Of the nine species known from the offshore islands, five (*Gonodactylus zacae*, *G. pumilus*, *Nannosquilla galapagensis*, *N. similis*, and *Heterosquilla insolita*) show strong American affinities. Only two of the nine, *Pseudosquilla adiastalta* (widespread on the offshore islands, see below) and *Neocoronida cocosiana*, appear to be closely related to Indo-West Pacific lineages.

The following stomatopod species are known from the offshore islands in the East Pacific; endemic species are marked with an asterisk (*).

Islas Tres Marias
- *Gonodactylus zacae*
- *Pseudosquilla adiastalta*

Islas de Revillagigedo
- *Gonodactylus zacae*

Clarion Island
- *Gonodactylus zacae*
- *Pseudosquilla adiastalta*

Clipperton Island

Pseudosquilla adiastalta
Cocos Island
**Neocoronida cocosiana*
Pseudosquilla adiastalta
Galapagos Islands
Coronida schmitti
**Gonodactylus pumilus*
Gonodactylus zacae
Heterosquilla insolita
Lysiosquilla sp. (larva)
**Nannosquilla galapagensis*
**Nannosquilla similis*
Pseudosquilla adiastalta
Pseudosquillopsis marmorata

Summary

A region of considerable zoogeographical importance, the East Pacific is inhabited by 50 species and subspecies of predaceous mantis shrimps (Stomatopoda, Crustacea). Many of these active and aggressive species show broadly overlapping ranges. However, even though sympatric, species may rarely encounter one another if they occupy different habitats. Analyzing the patterns of habitat use and frequency of co-occurrence of stomatopods in 19 localities in Pacific Costa Rica, we found that most species are associated with certain types of habitats. Upon a background of what is known of the biology of particular taxa, we examined the zoogeographic affinities of the East Pacific stomatopods.

Members of the Gonodactylidae inhabit holes and crevices, primarily in coral rubble and somewhat less frequently in rocks. Five of the six species recorded in this study were found at depths of less than 25 m. *Gonodactylus festae* had the narrowest depth distribution, and *G. zacae* had the broadest (0–64 m) (as well as the broadest geographic range) of the East Pacific gonodactylids. Members of this family were found either alone (only *G. zacae*) or with up to eight other species. Variable patterns of co-occurrence indicated loose associations between species and correlated with relative abundance. *Gonodactylus zacae* and *G. bahiahondensis* were the most abundant stomatopods recorded (along with *Meiosquilla oculinova*). Juvenile gonodactylids occurred in habitats appropriate for adults. Postlarvae are relatively small, and pelagic periods last for about a month in *Gonodactylus*. Although with American rather than Indo-West Pacific affinities, the eight East Pacific gonodactylids all are specifically distinct from their West Atlantic congeners. The color of the meral spots, used in displays of the raptorial appendage during fighting and mating, varies considerably in different species of closely related lineages.

Lysiosquillids burrow in sand, and in this study were found in association with coral rubble and rocks at the same sites with gonodactylids and some squillids. Also, the lysiosquillids were found in moderately shallow water (less than 25 m) and occurred in variable associations with up to eight other species. In contrast to the gonodactylids, the lysiosquillids exhibit little aggressive behavior. Two species of *Lysiosquilla*, two of *Coronida*, one of *Neocoronida*, and seven of *Nannosquilla* are endemic to the East Pacific. Species of *Coronida* and one *Lysiosquilla* show affinities to species in the East Atlantic; *Neocoronida* and the other species of *Lysiosquilla* are related to Indo-West Pacific species. *Nannosquilla* is American. However, of the two East Pacific species of *Heterosquilla* that occur in warm water, one is circumtropical and one also occurs in the West Atlantic. Also, both East Pacific species of *Acanthosquilla* are known from the West Atlantic as well. Planktonic larval periods probably are relatively long; the sizes of postlarvae vary from moderately small (*Acanthosquilla*) to large (*Lysiosquilla* and *Heterosquilla*).

Squillid species occupied the most variable habitat types. Two species, *Meiosquilla oculinova* and *M. swetti*, were strongly associated with crevices in rock and, to a lesser extent, coral rubble at less than 25 m; a third species, *M. dawsoni*, was found in a stream on an intertidal mudflat. Followed by *Gonodactylus zacae* and *G. bahiahondensis*, *Meiosquilla oculinova* was the most abundant stomatopod found in Costa Rica. In accordance with their habitat type, *M. oculinova* and *M. swetti* were found with one to eight other species of gonodactylids and lysiosquillids. Again, species associations were loose and related to relative

abundance; the most frequent species associations at different localities were *M. oculinova*, *Gonodactylus zacae*, and *G. bahiahondensis*. *Meiosquilla oculinova* exhibited moderate aggressive behavior. The remaining four species of squillids and two species of pseudosquillids occurred, frequently together, in deep (55–73 m), muddy environments. Larval and juvenile squillids were found in a diverse array of habitats, depths, and species associations. Pelagic periods of squillid larvae can last a number of months, and larvae settle at small to moderate (*Meiosquilla*) or moderate to large (*Squilla*) sizes. With Atlanto-American affinities, the three species of *Meiosquilla* and seven of the eight species of *Squilla* occur only in the East Pacific. However, one species of *Squilla* also is represented by a subspecies in the East Atlantic, and at least four species show close relationships to West Atlantic species. One species of *Cloridopsis* is known both from the West Atlantic and East Pacific. One species of *Clorida* occurs both in the East Pacific and the Indo-West Pacific, and two species of an endemic genus, *Schmittius*, have Indo-West Pacific affinities. Although the pseudosquillids have large postlarvae and probably have long larval periods, most species are endemic to the East Pacific. However, they show strong affinities to East Atlantic (*Pseudosquillopsis*), West Atlantic (*Parasquilla*), and Indo-West Pacific (*Pseudosquilla*) species.

Thirty eight (76%) of the 50 East Pacific stomatopods are endemic, and 45 of the 50 are warm-water species. Five of the latter are shared with the West Atlantic (11%), one (though subspecifically distinct) with the East Atlantic (2%), and two with the Indo-West Pacific (4%). Including shared and closely related species, 60% of those occurring in the East Pacific show closest affinities to West Atlantic taxa, 11% are most closely related to East Atlantic taxa, and 16% have closest ties to the Indo-West Pacific stomatopod fauna. Nine of the 50 East Pacific species occur on offshore islands where three are endemic, six show strong American affinities, and two are related to Indo-West Pacific species.

Appendix

Gazetteer

Coordinates for East Pacific localities mentioned in the text are listed below. All but those for San Diego were taken from gazetteers of the United States Board of Geographic Names; San Diego was located on a hydrographic chart. Alternate spellings are given in brackets.

California		
San Diego	32°42′N,	122°50′W
Chile		
Iquique	20°13′S,	70°10′W
Clarion Island (Mexico)	18°22′N,	114°44′W
Clipperton Island (France)	10°18′N,	109°13′W
Cocos Island (Costa Rica)	05°33′N,	86°59′W
Costa Rica		
Bahía Ballena	09°45′N,	85°01′W
Bahía Carrillo [Piedra Blanca Bay]	09°52′N,	85°30′W
Bahía de Salinas	11°03′N,	85°43′W
Golfo de Nicoya	09°47′N,	84°48′W
Isla Jasper	09°46′N,	84°54′W
Isla San Lucas	09°56′N,	84°54′W
Playa Blanca	09°22′N	84°08′W
Port Parker [?Golfo Elena]	10°56′N,	85°49′W
Puerto Culebra	10°39′N,	85°39′W
Puntarenas	09°58′N,	84°50′W
Uvita Bay [?Bahia de Coronado]	09°00′N,	83°50′W
Ecuador		
Bahía de Santa Elena	02°06′S,	80°53′W
Isla La Plata	01°16′S	81°06′W
El Triunfo	13°17′N,	88°33′W
Golfo de Fonseca	13°10′N,	87°40′W
Galapagos Islands (Ecuador)	00°30′S,	90°30′W
Isla Guadalupe (Mexico)	29°00′N,	118°16′W
Islas de Revillagigedo (Mexico)	19°00′N,	111°30′W
Islas Tres Marias (Mexico)	21°25′N,	106°28′W
Mexico		
Bahía Chamela	19°33′N,	105°07′W
Bahía Concepcion	26°39′N,	111°48′W
Bahía de La Paz	29°09′N,	110°25′W
Bahía de Petatlan	17°34′N,	101°30′W
Cabo San Lucas	22°53′N,	109°54′W
Guaymas	27°56′N,	110°54′W
Isla Angel de la Guarda	29°20′N,	113°25′W
Isla Espirito Santo	24°30′N,	110°22′W
Isla Isabela	21°51′N,	105°55′W
Isla San Francisco	24°50′N,	110°35′W
Los Palmillos, San José del Cabo	23°03′N,	109°41′W
Mazatlán	23°13′N,	106°25′W
Nayarit [?Tepic]	21°30′N,	104°54′W
Puerto Escondido	25°48′N,	111°20′W
Teacapán	22°33′N,	105°45′W
Panama		
Balboa	08°57′N,	79°34′W
Golfo de Chiriquí	08°00′N,	82°20′W
Isla Taboga	08°47′N,	79°33′W
Isla Taboguilla	08°48′N,	79°31′W
Peru		
Paita	05°56′N,	81°07′W
Tumbes	03°34′S,	80°28′W

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