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SURVEY OF THE SIPUNCULA OF THE CORAL AND BEACH-ROCK COMMUNITIES OF THE CARIBBEAN SEA

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ABSTRACT

Sipunculans inhabiting beachrock and coralline limestone have been collected from 36 stations in the Caribbean Sea and Straits of Florida. Eleven species have been identified; they belong to the genera *Aspidosiphon, Lithacrosiphon, Paraspidosiphon, Phascolosoma* and *Themiste*. The habitats are described, the species listed, and relative abundance and distribution of each species reviewed. Some general observations are reported on the biology of the most common species, including feeding patterns and possible mechanisms for formation of the burrows.

INTRODUCTION

While gathering material for a systematic and developmental study of the Sipuncula of the Caribbean Sea, I have collected numerous sipunculans from burrows in coralline limestone and beachrock at stations situated throughout the Caribbean Sea and Straits of Florida. In the course of these collections, observations have been made on various aspects of the biology of the rock-boring species, including their relative abundance, distribution, types of substrata inhabited (Rice 1969), structure of burrows, and in a few instances, feeding behavior. Eleven species, constituting 97 percent of those collected from calcareous substrata, will be considered here. They are, in order of abundance in the collection, as follows: *Phascolosoma perlucens* Baird, 1868; *Phascolosoma antillarum* Grube and Oersted 1859, *Lithacrosiphon gurjanovae* Murina 1967, *Aspidosiphon brocki* Augener 1903, *Paraspidosiphon steenstrupi* (Diesing 1859), *Paraspidosiphon fischeri* (Ten Brocke 1925), *Paraspidosiphon spinososcutatus* (Fischer 1922*a*), *Themiste alutacea* (Grube 1859), *Paraspidosiphon speciosus* (Gerould 1913), *Phascolosoma varians* Keferstein 1865, and *Paraspidosiphon klunzingeri* (Selenka and Bülow 1883). All of these species, with the exception of *Phascolosoma varians*, were always found in burrows in calcareous rock. *Phascolosoma varians* occurred in burrows only when the rock was soft and friable; otherwise it was found in gravel, under rocks, or in crevices. Of these 11 species, only *Paraspidosiphon klunzingeri* has not been reported previously in the

Caribbean Sea. The remaining three percent of the specimens are unidentified species of *Paraspidosiphon*, *Phascolosoma* and *Golfingia*.

In the past, three notable studies have been concerned specifically with the Sipuncula of the Caribbean. They are those of Fischer (1922*a*) on collections from Barbados and St. Thomas, Ten Broeke (1925) on collections from Curaçao, and Murina (1967) on collections from Cuba. Other records of specimens from this area are encountered in various reports on collections of museums or expeditions (see Keferstein 1867, Gerould 1913, Fischer 1922*b*). This report, covering a broader area of the Caribbean than previous accounts, provides additional information on the distribution patterns of the 11 rock-dwelling species mentioned above and also reviews the available information on several aspects of their biology, including their rock-boring activities. Taxonomic problems, mentioned briefly here, will be treated in detail in a later treatise on systematics.

MATERIALS AND METHODS

Sipunculans were collected at 36 stations in the Straits of Florida and Caribbean Sea. The distribution and number of stations were as follows: Florida, 7; Bimini, 2; Jamaica, 2; Puerto Rico, 9; Barbados, 5; Venezuela, 8; Curaçao, 3. Locations of the stations are indicated on the map (Figure 1) and in Table 1. The total number of recorded specimens was 3,423.

All specimens were taken from calcareous rock, usually in the intertidal or shallow subtidal waters. At six stations samples were taken at greater depths (8 to 75 feet) by dredging or diving. Habitats at the various stations included calcified mangrove reefs, fossil coral reefs (Fig. 2), recent coralline limestone, calcarenite boulders, beachrock (Fig. 3), coral rubble and dead portions of living coral colonies (Table 1). Texture of the substrata varied from the relatively soft and friable calcified mangrove reef to the hard and dense coral rock. Composition and characteristics of the substrata at several of these stations have been described in a previous paper (Rice 1969).

Animals were extracted from their burrows by fracture of the rock with geology pick and chisel and careful exposure of the burrows. Some specimens were maintained alive for developmental studies whereas others were preserved in 70 percent alcohol or in 10 percent neutral formalin or in a combination of the two. Prior to preservation, animals were relaxed in 10 percent alcohol in sea water. During the process of extraction from the rock many of the animals were unavoidably injured and those damaged beyond recognition were discarded.

Table 1 lists the station localities, station numbers used in these collections, habitat characteristics, and the number of each species collected at each station. In a few instances (indicated by +) the presence of a species was recorded but

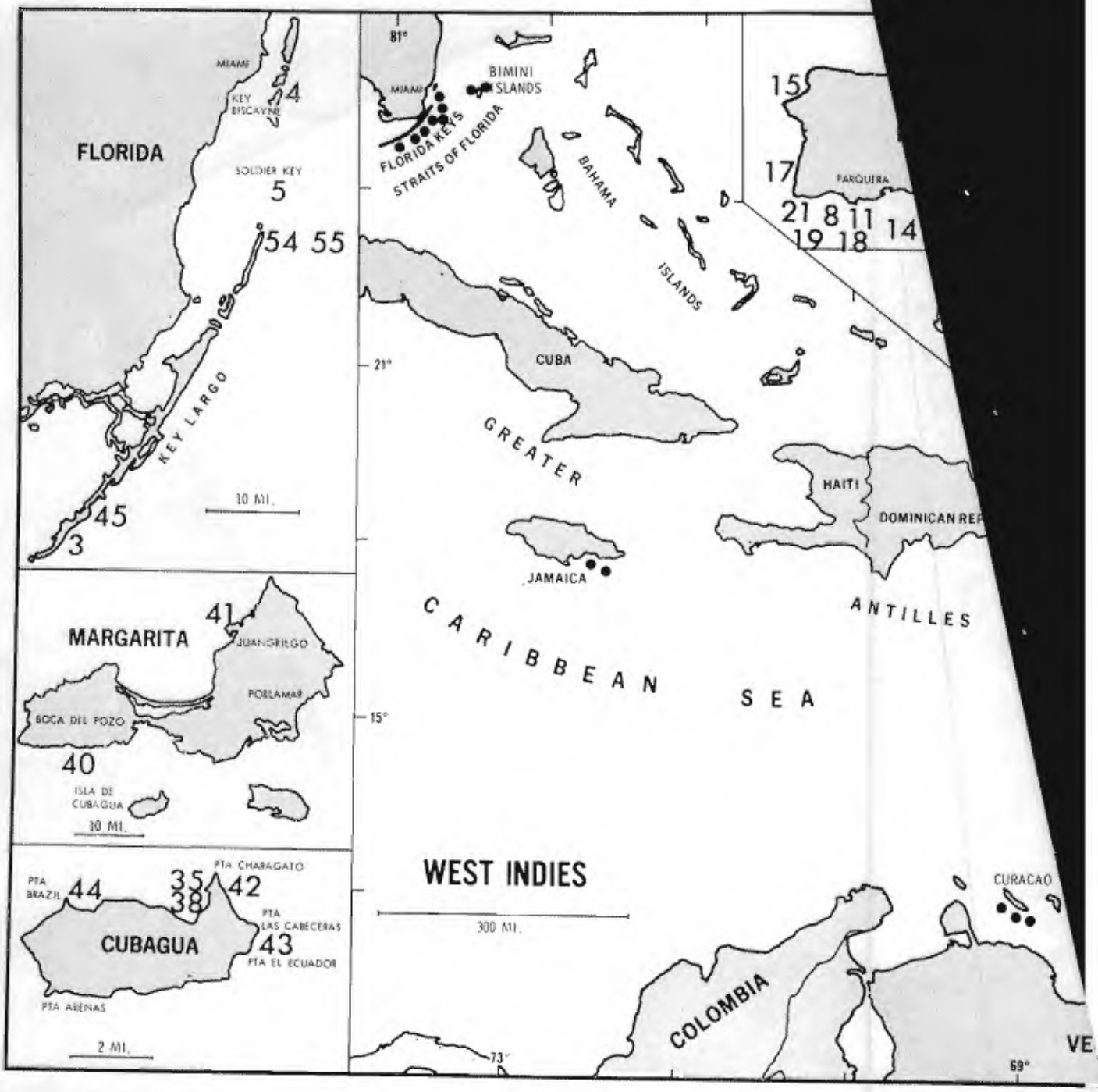
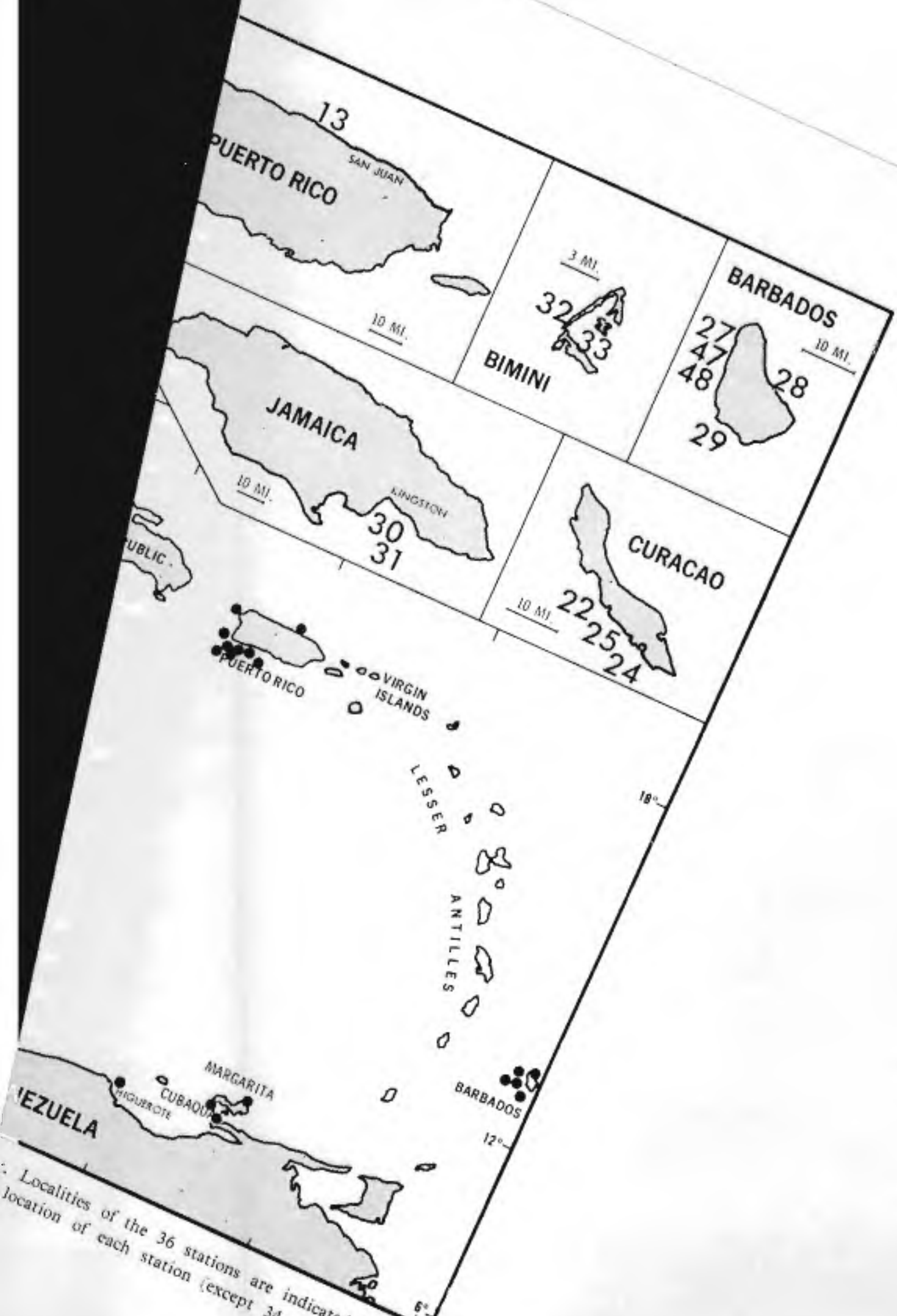


Figure 1. Map of the Caribbean Sea and adjacent waters showing locations of stations at which sipunculans were collected from calcareous ro
spheres (1). (The 5 stations at Cubagua, Venezuela are marked by a single sphere, due to limited space.) In the enlarged insets the more preci
signated by the station number (see Table 1).



. Localities of the 36 stations are indicated by solid location of each station (except 34 and 51) is de-

specimens were not saved and exact numbers were not available. The figures listed are interpreted only as an indication of relative abundance. Species density was determined at only one station, Cabo Rojo, Puerto Rico (see Results).

RESULTS

Phascolosoma perlucens (Fig. 4) (formerly known as *Phascolosoma dentigerum*, see Rice and Stephen 1970) was the most abundant species in the calcareous rock, constituting at least 46 percent of the specimens collected. Widely distributed, it occurred in Florida, Bimini, Jamaica, Puerto Rico, Barbados, Venezuela and Curaçao (Table 1). It was found at 94 percent of the stations in all types of rock from the exceedingly friable calcified mangrove reef and highly eroded limestone boulders to the hard, compact recent and fossil coral rock. Although most abundant in intertidal habitats, it was also present at depths of 75 feet. Usually *Phascolosoma perlucens* appeared in the same rock with one or more other species of sipunculans and commonly it was the dominant species.

Reflecting the shape and presumably the activity of the animals, the burrows of this species were found to be long, narrow and frequently winding with a single opening to the surface of the rock. With its anterior end always directed toward the opening the animal was tightly ensconsed within the walls of the burrow and when exposed or removed from the rock the body expanded to exceed considerably the diameter of the burrow. Animals maintained within rocks in the laboratory were observed to extend introvert frequently to the exterior, then retract it. When specimens were placed in artificially constructed burrows covered by glass slides, peristaltic movements of the body were noted (Rice 1969). In the laboratory, once removed from their burrows, the sipunculans crawled into cavities or crevices of various calcareous substrata provided for them, but they were never observed to form new burrows.

Observations on animals in intact burrows in the laboratory have shown that feeding is accomplished by extending the introvert at great distances from the mouth of the burrow over the surface of the rock, while accumulating small particles of detritus on the tentacles and hooks. The particles are engulfed when the introvert is retracted. Examination of gut contents of a few specimens immediately after collection from the field have revealed fragments of rock, unidentified fine particulate matter, algal strands, diatoms, foraminifera and a few small crustacean molts.

Previously this species has been recorded from only three localities in the Caribbean Sea: Jamaica (Baird 1868), Barbados (Fischer 1922*a*), and St. Barthelemy (Fischer 1922*b*). Ten Broeke (1925) described a similar but smaller species from Caracas Bay, Curaçao which she named *Phascolosoma microdentigerum*. Specimens

Localities and habitats of rock-dwelling sipunculans in collections from the Caribbean Sea and surrounding waters.

Station number	Locality	Habitat
4	FLORIDA Key Biscayne (NE shore)	calcified mangrove reef, intertidal
5	Soldier Key	fossil coralline limestone, intertidal
54	Bache Shoal	recent coralline limestone boulders, 8 feet
55	Triumph Reef	*Acropora* rubble, 25—30 feet
45	Key Largo (SE shore, 5 miles N of Tavernier)	fossil coralline limestone, intertidal
3	Key Largo (SE shore, Harry Harris Park)	fossil coralline limestone, intertidal
51	Pigeon Key	fossil coralline limestone, intertidal and subtidal
32	BIMINI North Bimini (NW shore)	calcarenite platform, intertidal
33	North Bimini (NE lagoon)	calcarenite boulders, subtidal
30	JAMAICA Drunkenman's Cay (near Port Royal)	coralline limestone boulders, intertidal and subtidal
31	Southeast Cay	coralline limestone boulders, intertidal and subtidal
13	PUERTO RICO Punta de Cerro Gordo (N coast, near San Juan)	calcarenite outcrop on exposed sandy beach, intertidal
15	Aquadilla (W coast)	sandstone conglomerate along exposed shore (between layers), intertidal
17	Boqueron Bay (W coast)	pitted coralline limestone boulders, subtidal
21	Cabo Rojo (SW coast)	pitted calcarenite boulders, intertidal
8	Arrecife Enrique (SW coast)	recent coralline limestone intertidal and subtidal
11	Mangrove Island (near La Parguero)	*Porites* rubble, intertidal
14	Cayo Turrumote (SW coast)	recent coralline limestone boulders, intertidal and subtidal
18	Outer deep reef (6 miles S La Parguera)	highly pitted coralline limestone boulders, 75 feet

TABLE I

Phascolosoma perlucens	*Phascolosoma antillarum*	*Lithacrosiphon gurjanovae*	*Aspidosiphon brocki*	*Paraspidosiphon steenstrupi*	*Paraspidosiphon fischeri*	*Themiste alutacea*	*Paraspidosiphon spinososcutatus*	*Paraspidosiphon speciosus*	*Phascolosoma varians*	*Paraspidosiphon klumpingeri*	*Paraspidosiphon* spp.	*Phascolosoma* spp.	*Golfingia* spp.	Total recorded specimens
171	23					3			5					202
26	1													27
(+)	1	2		2	1							3		9
2				2	3	1		1						9
2			4											6
26	2		79			3						1	1	112
(++)	1		12			3						1	1	18
12	2	(+)		2	2		9				1	2		30
1				4			22				1			28
5	3	9		3			8		(+)		3		3	34
6			56	3					2		3			70
18	50	1												69
13														13
9	(+)	18	16	3							1	1	3	51
67	276					1						8	1	353
36	2	1	35	2					4			1		81
1									6		1	2		10
5	2	5	19	1			5				2	2		41
1		6		4								1		12

Station number	Locality	Habitat
19	Arrecife Margarita (near La Parguera)	highly pitted coralline limestone boulders, 75 feet
27	BARBADOS Six Men's Bay (W shore)	beachrock, coarse-grained biocalcarenite, intertidal
47	Speightstown (W shore)	beachrock, coarse-grained biocalcarenite, intertidal
29	St. Lawrence Gap (S shore)	calcarenite boulders, intertidal
28	Bath (E shore)	highly pitted coralline limestone boulders, subtidal
48	Holetown (W coast, 1/2 mile from shore)	pitted coralline limestone boulders, 50—75 feet
40	VENEZUELA Isla Margarita, Boca Chica (SW shore)	calcarenite rock along exposed shore, intertidal
41	Isla Margarita, Playa Caribe (NE shore)	*Porites* rubble, subtidal
42	Isla Cubagua, Punta el Medio	coralline limestone boulders, 12 feet
35	Isla Cubagua, Punta Charagato	calcarenite rock along shore, intertidal
38	Isla Cubagua, Ens. de Charagato	calcarenite rock along shore, intertidal
43	Isla Cubagua, Punta el Ecuador	calcarenite boulders, intertidal and subtidal
44	Isla Cubagua, Punta Brazil	calcarenite boulders, intertidal and subtidal
34	Los Totumos (near Higuerote)	calcarenite boulders
22	CURAÇAO Piscadera Baai (S shore near mouth of bay)	coralline limestone boulders, intertidal
25	South shore, near Lagoen Jan Tiel	coralline limestone platform, intertidal
24	Spaansche Water (S shore)	*Porites* rubble, intertidal
		Total Number of Recorded Specimens
		Percent of Total Recorded Specimens

Subtidal refers to shallow subtidal from depths of 1 to 3 feet. (+) indicates that the presence of the species was recorded but specimens were not preserved; exact numbers are not available. Presence of the species was noted as either a few (+) or many (++) specimens.

Phascolosoma perlucens	*Phascolosoma antillarum*	*Lithacrosiphon guryanovae*	*Aspidosiphon brocki*	*Paraspidosiphon steenstrupi*	*Paraspidosiphon fisheri*	*Themiste alutacea*	*Paraspidosiphon spinososcutatus*	*Paraspidosiphon speciosus*	*Phascolosoma varians*	*Paraspidosiphon klunzingeri*	*Paraspidosiphon* spp.	*Phascolosoma* spp.	*Golfingia* spp.	Total recorded specimens
			2					4		1		1		8
686	18	32		8	7									751
24	3													27
21	28	5		7	1					1				63
12	8			6	12			9		1	2			50
16		4		19	6					3			1	49
12														12
5	37				2	18							3	65
	1					2								3
305	1				77	6						2		391
38	(+)				3	5								46
6	4					8								18
(+)	15				1									16
(+)	(++)					1					(+)			1
17	1	3		4										25
18	37			1								1		57
7	15	412	30	90	45		6	5			55	1		666
1568	531	498	253	161	160	51	50	19	17	6	69	27	13	3,423
45.8	15.5	14.6	7.4	4.7	4.7	1.5	1.5	0.6	0.5	0.2	2.0	0.8	0.4	

in my collections from Spaansche Water, Curaçao, in close proximity to the type locality of *P. microdentigerum*, could not be distinguished from *P. perlucens* found at other localities throughout the Caribbean region.

Phascolosoma perlucens is widely distributed in tropical waters. On the Pacific Coast of North America it has been found in the Gulf of California and in the Bay of Panama (Fisher 1952). It has been reported most often in the Indo-Pacific (see Selenka, de Man, and Bülow, 1883, Shipley 1898, Fischer 1922*b*, Edmonds 1956). Fisher (1952, p. 434) suggested that in the Indo-Pacific the species might be even more common than records indicated, but because of its habit of "hiding in crannies of coral rock", it was probably often overlooked. Perhaps the concealed nature of the habitat also explains the scarcity of previous records of this species in the Caribbean.

Phascolosoma antillarum (Fig. 5), the second most abundant species in the collections, comprised approximately 16 percent of the specimens collected. Distributed throughout the Caribbean and surrounding waters, it was found in Florida, Bimini, Jamaica, Puerto Rico, Barbados, Venezuela and Curaçao. Similar to *P. perlucens*, this species occurred in rocks of varying textures from soft and friable to hard and dense. Most commonly it inhabited the same rock as *P. perlucens*, although usually it occurred in smaller numbers. However, at two stations, Cabo Rojo, Puerto Rico, and Punta de Cerro Gordo, Puerto Rico, *P. antillarum* was by far the dominant species of sipunculan in the rock. The rock at Cabo Rojo was an intertidal pitted calcarenite boulder composed of calcite with some aragonite and some smoky quartz grains (Rice 1969). Comprising 70 percent of the sipunculans in the rock, *Phascolosoma antillarum* was present in a density of approximately 415 animals per square meter. The remainder of the sipunculans in the rock were *Phascolosoma perlucens* (101 per square meter) along with one specimen of *Themiste alutacea* and a few specimens of unidentified species. The rock at Punta de Cerro Gordo, Puerto Rico was situated intertidally along an exposed sandy beach as an outcrop of cemented calcarenite, composed of mostly aragonite with some high magnesium calcite (Rice 1969). Both *P. antillarum* and *P. perlucens* were abundant within the rock, but the former was by far the dominant species.

In contrast to those of *Phascolosoma perlucens*, the burrows of *P. antillarum* were usually straight and wide, decreasing in width anteriorly and terminating posteriorly as a rounded, cupulate chamber. Before removal from their burrows animals were observed to extend the tentacular crown with its numerous long filiform tentacles through the opening of the burrow to the surface of the rock, remaining in this position for several minutes at a time. It is presumed that the animals feed by a ciliary-mucus mechanism. Examination of the gut of a few specimens showed the contents to consist largely of a fine particulate matter with only a few small fragments of rock and few strands of algae. Compared with gut contents of *P. perlucens*, there was less diversity in size of particles and composition.

This species has been reported previously from many localities in the Caribbean region: Puerto Cabello, Venezuela, St. Croix (Grube and Oersted 1859), St. Thomas (Keferstein 1865, Fischer 1922*b*), St. Barthelemy (Fischer 1922*b*), Barbados (Fischer 1922*a*, Selenka, de Man and Bülow 1883, Gerould 1913), Jamaica (Baird 1868), Cuba, Colombia, Venezuela and Key West, Florida (Gerould 1913). In the Atlantic it has been found at Surinam and Brazil and in the Pacific at Baja California, Costa Rica, Panama and Chile, Hawaii and the Riukiu Islands (see Fischer 1952 for review of distribution). *Phascolosoma antillarum* is absent in the Indian Ocean and the Eastern Atlantic.

Lithacrosiphon gurjanovae (Fig. 6) was collected at stations in Bimini, Puerto Rico, Barbados, Jamaica, Curaçao and in the offshore coral reef of South Florida. It was absent from stations along the coast of Venezuela, including the islands of Margarita and Cubagua as well as the intertidal waters of the Florida Keys. Although the third most abundant species in the collections, comprising nearly 15 percent of the specimens collected, it was usually found in only small numbers. Its relative abundance in the total collections is explained by its great density at one station, Spaansche Water in Curaçao. Here in an intertidal bed of *Porites* it was the dominant species in the coral rubble and dead basal portions of living coral colonies. Other species of sipunculans occurring in the same habitat were, in order of abundance, *Paraspidosiphon steenstrupi*, *Paraspidosiphon fischeri*, *Aspidosiphon brocki*, *Phascolosoma antillarum*, *Phascolosoma perlucens*, *Paraspidosiphon spinososcutatus* and *Paraspidosiphon speciosus*. There were, in addition, many unidentified *Paraspidosiphon* (Table 1).

The burrows of *Lithacrosiphon* were short, straight and rounded posteriorly; even when exceedingly numerous as in the *Porites* rubble, they did not intersect (Fig. 7). The anterior shield, a cone-shaped structure with cuticular covering, was always directed toward the mouth of the burrow, apparently serving as an operculum. Frequently anterior cones were overgrown with coralline algae or, in some instances, with filamentous algae. *Lithacrosiphon gurjanovae* occurred in intertidal waters down to depths of 75 feet. It inhabited not only *Porites* rubble, as at Curaçao, but also, at other stations, it was found in recent coralline limestone boulders, pitted and eroded coralline limestone, and beachrock.

The following four species of *Lithacrosiphon* have been reported by other authors from the Caribbean: *L. alticonum* Ten Broeke 1925, *L. kukenthali* Fischer 1932*a*, *L. odherni* Fischer 1922*b*, *L. poritides* Ten Broeke 1925. All of the specimens noted in this paper have been interpreted to be one species, corresponding most closely to Murina's description (Murina 1967*a*) of *L. gurjanovae*. This species has been reported previously only from Cuba and is presumably endemic to the Caribbean.

Specimens of *Lithacrosiphon* in my collections from Spaansche Water, Curaçao differed from Ten Broeke's descriptions of *L. alticonum* and *L. poritides* from

Caracas Bay, Curaçao, although the two localities are adjacent to one another. The hooks of the introvert of *L. alticonum* were described by Ten Broeke as one-pointed on the anterior introvert and two-pointed posteriorly whereas in *L. poritides* all of the hooks were described as one-pointed. In specimens from Spaansche Water I found the anterior hooks to be two-pointed and the posterior hooks one-pointed. These discrepancies point to the necessity for a review of the genus *Lithacrosiphon* and a re-examination of Ten Broeke's type specimens.

Aspidosiphon brocki and *Paraspidosiphon fischeri* (Fig. 8) are both small species of approximately the same size, attaining a length of about 10 mm. Found at 25 percent of the stations, *A. brocki* comprised seven percent of the specimens collected and *P. fischeri*, occurring at 33 percent of the stations, comprised nearly five percent of the total specimens. Although there was some overlap in distribution, *A. brocki* occurred with greatest frequency in the northern Caribbean and Straits of Florida, whereas *P. fischeri* was found most often and in greatest numbers in the southern Caribbean in islands off the coast of Venezuela. Both species were present in Curaçao, but only *P. fischeri* was found at Cubagua, Venezuela and Barbados, and only *A. brocki* in Puerto Rico, Jamaica and the littoral waters of the Florida Keys. *Aspidosiphon brocki* occurred only in substrata of dense, compact coralline limestone or coral rubble, whereas *P. fischeri*, while found in similar substrates, also occurred in the coarse-grained biocalcarenite (beachrock) at Barbados and in the coarse conglomerate rock at Cubagua, Venezuela. The burrows of these small species were always located near the surface of the rock.

Aspidosiphon brocki was first described by Augener in 1903 from Indonesia (Amboina, Polo Edam) and not recorded again until Murina reported it from Cuba in 1967. *Paraspidosiphon fischeri*, first described from Curaçao in 1925 by Ten Broeke, is endemic to the Caribbean. Murina (1967*a*, *b*) described a subspecies, *Paraspidosiphon fischeri cubanus*, from Cuba.

Paraspidosiphon steenstrupi (Fig. 9) was present at stations in Bimini, Puerto Rico, Barbados, Jamaica, Cubagua (Venezuela) and Curaçao. It was notably absent only in the littoral waters of the Florida Keys. Rarely occurring in great numbers, it constituted only five percent of the total specimens collected. This species inhabited rocks of varying texture from the coarse-grained biocalcarenite of the beachrock of Barbados to the dense coralline limestone found at many stations throughout the Caribbean (Table 1). The characteristic anterior shield of *P. steenstrupi*, surrounded by a thickened rim, was often covered by calcareous deposits and occasionally with filamentous algal growth. Because of its position at the mouth of the burrow, the anterior shield has been assumed to serve as an opercular device. The posterior shield of this species was found to vary in shape from flattened to rounded to pointed, depending on the state of contraction at the time of preservation.

Other records of *P. steenstrupi* in the Caribbean are from Barbados (Fischer 1922*a*), St. Barthelemy, St. Thomas (Fischer 1922*b*), Curaçao (Ten Broeke 1925)

Figure 2. Fossil coralline limestone, intertidal. Key Largo, Florida (Station 3).

Figure 3. Beachrock, coarse-grained biocalcarenite. Six Men's Bay, Barbados (Station 27).

Figure 4. *Phascolosoma perlucens.*

Figure 5. *Phascolosoma antillarum.*

Figure 6. *Lithacrosiphon gurjanovae*

Figure 7. Burrows (indicated by arrows) of *Lithacrosiphon gurjanovae* in *Porites* rubble from Spaansche Water, Curaçao (Station 24). Rubble was broken open to expose burrows and animals removed

Figure 8. Left, *Paraspidosiphon fischeri.* Right, *Aspidosiphon brocki.*

Figure 9. *Paraspidosiphon steenstrupi.*

Figure 10. *Paraspidosiphon spinososcutatus.*

Figure 11. *Themiste alutacea.*

Figure 12. *Paraspidosiphon speciosus.*

The scale equals 2 mm on all figures.


4


5


6


7


8


9


10


11


12

and Cuba (Murina 1967*a*). With the exception of the Eastern Pacific this species has been reported in tropical waters around the world and has been considered as one of the commonest sipunculans in the Indo-Pacific (Shipley 1903, Sato 1939).

The remaining five species altogether make up less than five percent of the total specimens collected. *Paraspidosiphon spinososcutatus* (Fig. 10), accounting for 1.5 percent of the total, was found in both the southern and northern Caribbean, including stations at Curaçao, southwestern Puerto Rico, southeastern Jamaica, and Bimini. The substrata inhabited by this species were coral rubble and dense coralline limestone boulders from intertidal or shallow subtidal waters. *Paraspidosiphon spinososcutatus* was first described by Fischer (1922*a*) from Barbados and St. Thomas and later by Murina (1967*a*, *b*) from Cuba and the Gulf of Mexico. It is apparently endemic to the Caribbean Sea and nearby waters.

Themiste alutacea (Fig. 11), never found in great numbers, comprised 1.5 percent of the specimens collected. Its habitats varied from the soft and friable calcified mangrove reef to the hard and compact coral rubble or coralline limestone. Other localities in the Caribbean from which *T. alutacea* has been reported in the past are St. Croix (Grube and Oersted 1859) and St. Barthelemy (Fischer 1922*b*). In Florida it has been found at Cedar Keys, Key West and Dry Tortugas (Gerould 1913). The northernmost record in the Atlantic is Cape Hatteras (Gerould 1913) and the southernmost at Rio de Janeiro, Brazil (Selenka, de Man and Bülow 1883).

Paraspidosiphon speciosus (Fig. 12) and *Paraspidosiphon klunzingeri* together comprised 0.7 percent of the total specimens collected. Similar in gross external morphology, the two species are distinguished on dissection by the rectal caecum which is highly lobulated in *P. klunzingeri*, but simple in *P. speciosus*. There is also a striking difference in the shape of the hooks of the introvert. The hooks of *P. klunzingeri* have a blunter terminal point, a relatively broader base and are not as strongly bent as those of *P. speciosus*.

Paraspidosiphon speciosus was collected at offshore reefs of southern Florida and southwestern Puerto Rico and along the coasts of eastern Barbados and southern Curaçao. *Paraspidosiphon klunzingeri* was found at the same stations in Puerto Rico and eastern Barbados and at two additional stations in western and southern Barbados. At Curaçao *P. speciosus* occurred in intertidal *Porites* rubble in association with large numbers of other sipunculans (Table 1). At other stations the rocks in which these two species were found were highly pitted dead coral boulders with varying degrees of cementation and relatively low densities of sipunculan fauna.

Paraspidosiphon speciosus was first described by Gerould (1913) from Key West Florida, Cuba and Brazil. Later Fischer (1922*a*) reported its occurrence at St. Thomas. The distribution of *P. klunzingeri*, on the other hand, is widespread, although centered in the Indo-Pacific. It has been reported from the Red Sea (Selenka, de Man and Bülow 1883, Wesenberg-Lund 1957) to the Western Pacific (Shipley 1898) and the Great Barrier Reef, Australia (Edmonds 1956). In the At-

lantic it has been found at Liberia and the Cape Verde Islands (Wesenberg-Lund 1959).

Phascolosoma varians constituted 0.4 percent of the total specimens collected. It was collected at stations in Florida, Puerto Rico and Jamaica. It occurred burrowed within the rock at only one station at Key Biscayne, Florida where the rocky substratum consisted of a calcified mangrove reef of soft texture and loosely cemented structure. At stations near Port Royal, Jamaica this species was found in the crevices of dead coral boulders; at stations along the southwestern coast of Puerto Rico near La Parguera, it occurred sometimes in rock crevices or buried in a substratum of coarse sand and coral rubble or wedged between the branches of *Porites* rubble.

Phascolosoma varians has been reported from the Bahamas (Shipley 1890) and from Florida at Key West, Cape Florida, Key Vacas, Tortugas, Bird Key (Keferstein 1867, Gerould 1913, Fischer 1922*a*), as well as from numerous other localities throughout the Caribbean: St. Thomas (Keferstein 1865, Fischer 1922*a*), St. Croix (Grube and Oersted 1859, Keferstein 1865), Barbados, Jamaica (Fischer 1922*a*), St. Barthelemy, Haiti (Fischer 1922*b*), and Curaçao (Ten Broeke 1925). Although centered in the West Indies, it has been found at Bermuda and the Ascension Islands (Gerould 1913) and in the Pacific at Rotuma and Funafuti (Shipley 1898) and Formosa (Sato 1939).

DISCUSSION

Sipunculans are common inhabitants of the coral and beachrock communities throughout the Caribbean and nearby waters. Often occurring in great densities, they dwell in burrows, presumably of their own formation, within a variety of calcareous substrata.

The substrata varied widely in texture and hardness. Usually several species inhabited a single rock and dominance of a particular species showed no apparent association with type of substratum. Most species were found in both hard and soft calcareous substrata, but *Aspidosiphon brocki*, *Paraspidosiphon speciosus* and *Paraspidosiphon klunzingeri* were collected only from dense coralline limestone and *Phascolosoma varians* was burrowed only within soft calcareous rocks. As demonstrated in an earlier paper (Rice 1969), *Phascolosoma perlucens*, *Phascolosoma antillarum*, *Lithacrosiphon gurjanovae* and *Paraspidosiphon steenstrupi* all inhabit rocks of both friable and compact textures, containing calcite as well as aragonite. The greatest diversity of species in these collections was in the intertidal *Porites* rubble and dead basal portions of living *Porites* colonies at Spaansche Water, Curaçao (Table 1).

Although the rock-boring sipunculans reported here were found at all depths at which collections were made (intertidal to 75 feet), they occurred with greatest

abundance and diversity in intertidal waters. There was no specific correlation with depth in the range studied and with two exceptions all species collected in deeper waters also occurred intertidally. Two species, *Paraspidosiphon spinososcutatus* and *Phascolosoma varians*, were found only in intertidal or shallow subtidal waters; however, these same species have been reported by previous authors from deeper waters: 40 and approximately 30 meters, respectively (Murina 1967*b*, Fischer 1922*b*).

Of the 11 species of rock-dwelling sipunculans listed in this report, the following three are endemic to the Caribbean and surrounding waters: *Lithacrosiphon gurjanovae*, *Paraspidosiphon fischeri* and *Paraspidosiphon spinososcutatus*. Two other species, *Themiste alutacea* and *Paraspidosiphon speciosus*, are restricted to the Caribbean adjacent Atlantic coastline; both occur as far south as Brazil and the former has been recorded as far north as Cape Hatteras, North Carolina. The remaining six species have a wide distribution in tropical waters, all having been reported from the Pacific Ocean and some from the Indian Ocean as well.

In looking at reproductive patterns for possible factors influencing distribution, we find that *Themiste alutacea*, with a restricted distribution, has a short-lived lecithotrophic pelagic larval stage (Rice, elsewhere in this Symposium). On the other hand, the three species of *Phascolosoma (P. perlucens*, *P. antillarum* and *P. varians)*, with relatively wide distributions, all have long-lived planktotrophic larvae; the larva of *P. perlucens* has survived as long as six months in the laboratory. Information is available on reproduction of two Caribbean sipunculans, *Paraspidosiphon fischeri* and *Aspidosiphon brocki*, but no correlation with distribution is evident. *Aspidosiphon brocki*, recorded from both the Caribbean and the Pacific, reproduces asexually in the latter locality; sexual reproduction has not been observed. *Paraspidosiphon fischeri*, as in the case of the species of *Phascolosoma*, has a planktrotrophic pelagic larval stage, presumably capable of long survival, however, this species is endemic to the Caribbean region.

The remarkable abundance of *Phascolosoma perlucens* throughout the coral and beachrock communities of the Caribbean may be related, at least in part, to a prolonged breeding season. Although no single population was observed for a full year, this species was found to spawn in different localities in the Caribbean at every season. The second most abundant species, *Phascolosoma antillarum*, although observed with the same frequency and in the same localities, spawned only one time in the month of July.

Limited observations on feeding of two of the rock-boring species suggested differences in feeding behavior. *Phascolosoma antillarum*, a species with well-developed tentacular crown composed of numerous long, filiform tentacles appeared to feed by a ciliary-mucus mechanism, extending its tentacles to the exterior of the burrow for long periods. *Phascolosoma perlucens*, on the other hand, with fewer and much shorter tentacles, but a more extensible introvert, apparently fed actively on

detritus which it accumulated as small particles on the tentacles and hooks as the introvert was extended and retracted over the surface of the rock.

The structure of the burrows of rock-boring sipunculans and possible mechanisms by which the burrows may be formed have been the subjects of recent reports (Rice 1969, Rice and Macintyre 1972). Burrows are characterized by smooth linings which clearly truncate the microscopic grains of the rock. They may extend at any angle from the surface of the rock and only rarely, in densely populated rock, do the burrows intersect. Each burrow has one opening; the sipunculan is situated within the burrow so that its anterior end is directed toward the opening. Animals fit tightly within the burrows, the shape of the burrow reflecting that of the species. Thus, the burrow of *Phascolosoma perlucens* is long, narrow, and frequently sinuous, that of *P. antillarum* is broad and straight, terminating posteriorly in a rounded blind end, and that of *Lithacrosiphon gurjanovae* is short, straight and also rounded posteriorly.

Based on studies of the morphology of possible boring structures of the animal and on analyses of the walls of the burrows in rock-thin sections, it has been supposed that both chemical and mechanical mechanisms may be utilized by sipunculans in the formation of burrows in calcareous substrata (Rice 1969, Rice and Macintyre 1972). Although experimental evidence is lacking, it has been suggested that secretions of the numerous epidermal glands opening through the integument may be a possible source for chemical dissolution of the rock. Moreover, it has been postulated that mechanical abrasion might be effected by the frictional movement of thickened cuticular structures such as papillae and posterior shields against the walls of the burrows. Microscopic examination of the walls of the burrows has revealed alterations in the structure of the constituent grains, suggesting a chemical dissolution of the rock. At the same time, mechanical abrasion is also suggested by the occurrence of finely comminuted carbonate grains in the microscopic pockets of the walls of the burrows.

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