

Zoogeography of Marine Gastropod in the Southern Caribbean: A New Look at Provinciality

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ABSTRACT. – Recorded occurrences of 266 species of higher Gastropoda were arranged in nine subareas along the coastal areas of southern Central America and northern South America. The value of different gastropod families as zoogeographic indicators and the degree of faunal “singularity” of subareas were inferred respectively from the mean value of the index of “Breadth of Geographic Range” (BGR) of species involved. BGR was lower among families exhibiting predominantly direct development. About 43% of species are widely distributed in the tropical Western Atlantic, whereas approximately 40% are endemic to the southern Caribbean – enough to consider this area as a separate zoogeographic province. Northern Venezuela, Santa Marta, and the Leeward Islands are the subareas richest in species, whereas the subarea between the Orinoco delta and Surinam is the most depauperate. The number of species occurring in a given subarea is more closely related to environmental heterogeneity than to the shelf extent of the subarea. A similarity level of 50% distinguishes five zoogeographic areas within the lower Caribbean, two of them as transitional to other tropical Western Atlantic Provinces and the other three are proposed as subprovinces. Trade wind-induced upwelling along the coasts of northern Colombia and Venezuela on the one hand, and zoogeographic links of the present molluscan fauna to the Eastern Pacific on the other, are the main factors explaining the present distribution patterns of marine gastropod in the southern Caribbean.

RESUMEN. – Los registros de 266 especies de gasteropodos superiores fueron agrupados en 9 subareas a lo largo de las costas del Caribe entre el sur de **Centroamérica** y el norte de **Suramérica**. El valor de las diversas familias de **gasterópodos** como indicadores **zoogeográficos** y el grado de “singularidad” **faunística** de las subareas fue deducido a partir del valor promedio del índice de “Amplitud del Rango **Geográfico**” (ARG) de las especies incluidas. El ARG fue menor en las familias con desarrollo larval directo. El 43% de las especies **están** ampliamente distribuido en el **Atlántico** Occidental tropical y el 39.8% son **endémicas** del sur del Caribe – suficientes para considerar esa area como una provincia **zoogeográfica** aparte. Venezuela, Santa Marta y las Islas de Sotavento son las subareas con mayor numero de especies, mientras que la subarea comprendida entre el delta del Orinoco y Surinam es la **más** pobre en especies. El **número** de especies en una determinada **subárea está más** relacionado con el grado de heterogeneidad ambiental que con las dimensiones de la misma subarea. Un nivel de similaridad del 50% define cinco areas **zoogeográficas** en el sur del Caribe, dos de ellas consideradas zonas de transición hacia otras provincial del **Atlántico** Occidental tropical y otras tres propuestas como subprovincias. La surgencia inducida por los vientos alisios en las costas septentrionales de Colombia y Venezuela, y las relaciones **zoogeográficas** de la malacofauna actual con la del **Pacífico** Oriental, son los factores que mejor explican los esquemas actuales de distribución de los **gasterópodos** marinos en el sur del Caribe.

INTRODUCTION

The coastal and shelf areas of southern Central America and northern South America as far as the Orinoco delta are known as the southern Caribbean marine region. This area was frequently disregarded from biotic and biogeographic studies, and its fauna considered as “typical” West Indian-Caribbean (Houbrick, 1968; Bayer et al., 1970; Briggs, 1974), although Rehder (1962) and Work (1969)

stated that better knowledge of the fauna of the lower Caribbean could result in dividing the region into zoogeographical subregions. Meyer (1973) and Moore (1974) first referred to the coexistence of wide-ranging Caribbean species with remarkably high numbers of poorly known endemic elements along the shores of northernmost South America. More recently, based on molluscan distributions, Cosel (1976, 1982, 1986), Petuch (1976, 1981,

1982a, b, 1987, 1990), Gibson-Smith and Gibson-Smith (1979), and Díaz and Getting (1988) provided further evidence that certain areas in the southern Caribbean exhibit a somewhat "anomalous" faunal composition. Many endemic molluscan species have been described in the last two decades from the southern Caribbean (e.g., Bayer, 1971; Altena, 1975; Petuch, 1979, 1987, 1990; Díaz and Velásquez, 1986; Jong and Coomans, 1988).

The purpose of this paper is to document the faunal heterogeneity along the southern Caribbean coasts, and to test the somewhat intuitively claimed existence of molluscan faunules or "anomalously" composed areas, and its significance as zoogeographic areas. The analysis is based on the recorded occurrences of species from selected families of prosobranch gastropod that can be considered zoogeographic "indicators." The origin of the present biogeographic relationships of molluscan faunas in the southern Caribbean are discussed according to the emerging ideas.

METHODS

Selection of Taxa. —Marine molluscs, particularly gastropod, have been traditionally used for determining paleobiogeographic and zoogeographic patterns (e.g., Coomans, 1962; Hall, 1964; Woodring, 1974; Petuch, 1982a, b; Kohn, 1990). Many neogastropods exhibit a non planktonic developmental mode or have lecithotrophic larvae with very low dispersal capacity (cf. Radwin and Chamberlain, 1973), so they are often very restricted in their habitat preferences. The durable shells of most prosobranch gastropod preserve well as fossils and allow direct access to the paleobiogeographical record. Furthermore, gastropod are common collecting objects, thus systematic lists or species inventories are available for many areas.

Twenty-two families of higher caenogastropods were selected. All but two, Cypraeidae and Ficidae, belong to the Neogastropoda. Some families, such as Nassariidae and Turridae, were not included because most of their members are too small (less than 5 mm) and taxonomically very controversial, so that they are often dis-

regarded or misnamed in species lists. This criterion was also used to exclude several species belonging to the families Columbellidae, Vexillidae, and Marginellidae. The species chosen inhabit exclusively coastal habitats and the upper shelf zones to 100 m, for at least part of their range. Deeper occurring species have been often recorded only from a few localities.

Recent works including lists of gastropod species from the countries of this region and additional records, plus species inventories from various localities were used to develop a composite list of species that occur in the region (see Appendix). Emphasis was placed on revisionary works such as Vokes and Houart (1986) and Vink and Cosel (1985) rather than more general works. Especial caution was devoted to selecting the species described recently by Petuch (1987, 1990), as some of them (mainly in the families Olividae and Conidae) were described on the basis of subtle shell characters of single specimens falling into the variation range of known taxa. Only records where a species was specifically listed from an area were used; distribution maps suggesting that the range of a species should include one of the areas examined, but not specifying a locality, were disregarded.

Subareas. —Although the term "Southern Caribbean" refers conventionally to the area south of latitude 15°N to the continental coasts of Central and South America (from the Honduras-Nicaragua boundary to Trinidad), for the purposes of this paper the "Southern Caribbean" embraces the shores and shelf areas along the continental coasts of Central and South America, from northern Costa Rica to Surinam-French Guiana, including the Leeward Antilles off Venezuela (Aruba, Bonaire, Curaçao, Margarita, and other smaller Venezuelan islands). Nicaragua and Trinidad have been disregarded, because data on their molluscan faunas are very scarce. However, since the molluscan fauna of the area between the Orinoco delta and Surinam has been adequately documented, it has been included for this analysis.

According to broad environmental features and the availability of faunal infor-

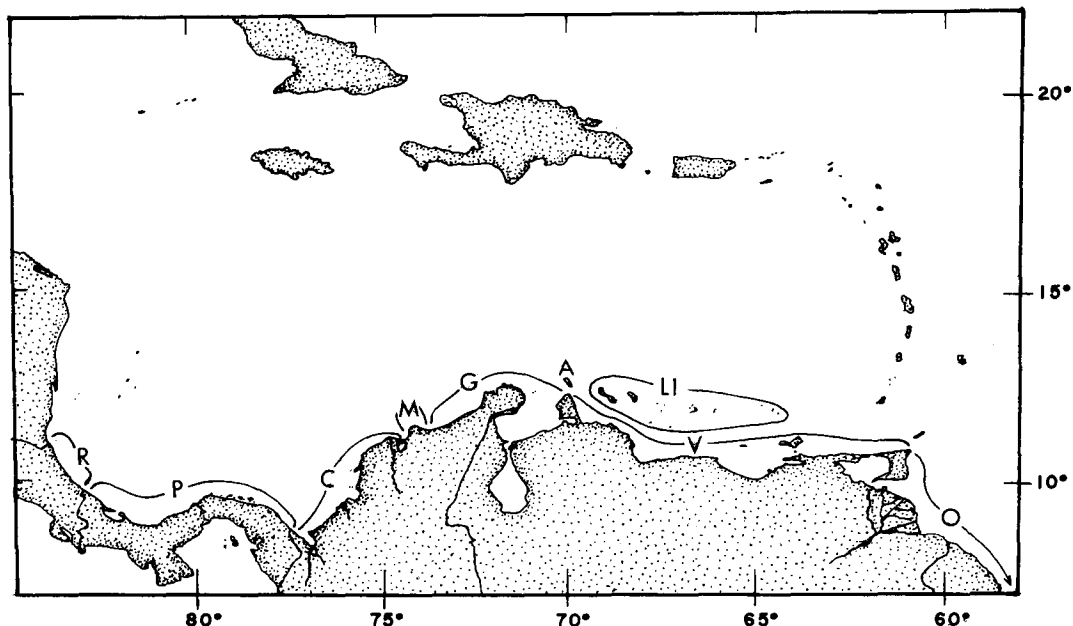


FIG. 1. The nine subareas selected for the analysis. A, Aruba; C, southern half of the Colombian Caribbean coast; G, Goajira and Paraguana peninsulas; LI, Leeward Islands; M, Santa Marta; O, Orinoco delta-Surinam; P, Panama; R, Costa Rica.

mation, the region was partitioned into nine subareas (Fig. 1). This paper compares the molluscan composition of these subareas. The data available from Costa Rica and Panama does not allow the creation of more subareas there, since most of the literature or specimen records list simply "Panama" or "Costa Rica" as collecting sites. Aruba (A) has been singled out from the remainder Leeward Islands because "its marine fauna is to certain degree distinct from that of Curaçao and Bonaire" (Jong and Coomans, 1988). Furthermore, the sea floor around these islands drops away rapidly to a depth of almost 1000 m, whereas the maximum depth between Aruba and the Venezuelan coast does not exceed 135 m. A small portion of the Caribbean coast of Colombia from the vicinity of Santa Marta eastwards to the sector where the easternmost spurs of the Sierra Nevada de Santa Marta drop into the sea has been also singled out (M), as it represents a well documented distributional boundary for some molluscs (Cosel, 1976, 1982, 1986; Díaz and Getting, 1988; Díaz, 1990). Colombia and Venezuela have or share three subareas,

which can be recognized on the basis of both ecological and faunal features. An outline of the environmental features of each subarea is presented in Table 1.

Comparative Analysis.— I used Czechanovsky's presence-absence index of similarity, which is widely used to determine affinities among biotic assemblages, and is also employed to compare species overlap between geographic areas (e.g., Crovello, 1981; Wells, 1990). The formula is:

$$S = \frac{2c \times 100}{a + b}$$

where a is the number of species in subarea A, b the number in subarea B, and c the number of species in common. The index ranges from 0 (no species in common) to 100 (total overlap). A dendrogram was produced from the similarity matrix using the group-average sorting strategy.

Since most species do not occur throughout the region and many are even endemic to a subarea (or their range in the Lower Caribbean embraces only one or a few of the subareas), every species does not have the same value as indicator for defining

TABLE 1. Major environmental features of the shelf, shores, and water masses in the subareas examined (extracted from IUCN [1979] and Wells [1988]).

	Shelf, bottom	Water	Habitats
R (Costa Rica)	Narrow; mud, sand	Calm to agitated; turbid and somewhat brackish in the north, rather clear in the south	Estuaries; scattered mangroves sandy shores; seagrass; poorly developed coral reefs
P (Panama)	Narrow; fringing coralline archipelago; mud, sand, gravel bottoms	Predominantly clear; rather calm	Well developed coral reefs; mangroves; seagrass; scattered rocky and sandy shores
C (Southern Colombia)	Rather narrow; predominantly mud	Calm; predominantly turbid; influenced by discharges of major river systems	Estuaries; mangroves; scattered seagrass-meadows and coral reefs around offshore islands; sandy shores
M (Santa Marta)	Extremely narrow to absent; steep; mud, sand, gravel	Agitated to calm; rather clear to turbid; seasonally affected by upwelling	Rocky shores; fringing reefs; scattered seagrass meadows; mangroves, and sandy shores
G (Goajira-Paraguana)	Rather narrow to wide; sand, gravel, mud	Agitated; turbid; somewhat brackish in the north; permanently affected by upwelling	Sandy shores; seagrass; scattered mangroves; algae meadows
A (Aruba)	Narrow; sand, gravel, rocks	Clear; agitated to calm	Sandy shores; coral reefs; mangroves; seagrass
LI (Leeward Islands)	Absent; steep; sand, gravel, rocks	Clear; agitated to calm	Rocky and sandy shores; well developed reefs; mangroves; seagrass
V (Central Venezuela)	Very irregular; absent to very wide; mud, sand, gravel, rocks	Rather turbid; agitated; affected by upwelling in the eastern part	Rocky and sandy shores; scattered seagrass and mangroves; poorly developed coral reefs
O (Orinoco-Guiana)	Very wide; predominantly mud	Turbid; agitated; somewhat brackish; affected by discharges of major river systems	Sandy and gravel shores; estuaries

the degree of faunal "singularity" of a given subarea. Consequently, each species was given an equitable value according to the extent of its geographic range within the region. The "Index of Breadth of Geographic Range" (BGR) of a species is defined as the percent of the total number of subareas (or sites) considered in the analysis (nine in this case) occupied by a species.

RESULTS

The 266 species considered in this study (see Appendix) inhabit diverse coastal and shelf environments, including rocky

shores, coral reefs, mangroves, seagrass meadows, sand, muddy, gravel, and rubble bottoms. Most species range in depth between 2 and 50 m, and only few inhabit exclusively shallower (e.g., *Purpura patula* and *Terebra salleana*) or deeper waters (e.g., *Fulgurofusus brayi* and *Fusinus couei*). The great majority of the species are predators on worms and other molluscs, some are scavengers, and a handful occasionally eat plant material. Shell size ranges from less than 5 mm (several Columbelloidea and Marginelloidea) to more than 400 mm (Turbinelloidea).

Table 2 summarizes the number of gen-

TABLE 2. Number of genera, mean value of the index of Breath of Geographic Range (BGR) of the species, total number of species, and distribution of the number of species in the nine subareas examined.

Families	Number of		Mean BGR	Number of species in subareas									
	Gen- era	Spe- ties		R	P	C	M	G	A	L	I	V	O
Cypraeidae	2	6	36.1	3	4	5	4	6	4	4	4	4	1
Ficidae	1	2	26.7	0	0	0	0	1	1	0	2	1	
Muricidae	18	45	22.9	11	15	11	17	18	10	18	24	15	
Thaididae	2	7	34.6	4	5	7	4	1	4	4	4	3	
Colubrariidae	1	3	38.5	1	2	2	3	1	2	2	1	1	
Columbellidae	10	33	31.3	19	15	19	14	19	18	18	18	4	
Melongenidae	2	2	36.4	1	1	1	1	1	1	1	2	2	
Buccinidae	8	18	20.5	7	8	7	9	10	11	8	11	0	
Fasciolaridae	8	17	23.1	4	7	5	10	8	8	9	10	4	
Columbariidae	1	1	44.4	0	1	1	0	1	0	0	1	0	
Volutidae	3	6	14.7	2	2	2	1	1	1	1	2	0	
Harpidae	2	2	19.0	1	0	1	2	1	1	1	1	0	
Cancellariidae	3	3	20.0	1	0	1	2	1	0	0	2	1	
Turbinellidae	2	4	26.5	2	2	2	2	2	2	1	2	1	
Olividae	5	24	21.7	5	9	9	11	7	12	6	10	5	
Marginellidae	9	30	20.0	5	7	9	10	7	13	14	9	3	
Volutomitridae	1	2	16.7	0	1	0	0	2	0	0	1	0	
Mitridae	1	3	25.5	2	3	2	1	0	2	1	2	1	
Vexillidae	4	19	18.1	6	5	2	10	2	11	8	5	1	
Costellariidae	2	3	9.5	0	0	0	0	3	0	0	1	0	
Conidae	1	28	20.5	8	10	10	14	12	11	12	6	6	
Terebridae	3	8	31.6	2	5	4	5	4	5	4	6	2	
	89	266	$\bar{x} = 23.8$	81	102	100	120	108	117	112	124	51	

era, the average for the species in each family, as well as the number of species in the nine subareas. The 22 families considered for the analysis yielded 266 species belonging to 89 genera. Five families contributed more than 60% of the species: Muricidae (16.9%), Columbellidae (12.4%), Marginellidae (11.3%), Conidae (10.5%), and Olividae (9%). The genera *Steironepion*, *Nassarina*, *Aesopus* (Columbellidae), *Volvarina*, and *Gibberula* (Marginellidae) were omitted because they are too small and poorly understood.

Of the 266 species, 115 (43%) are widely distributed in the tropical Western Atlantic. Five occur also in the Eastern Atlantic (Amphiatlantic species) and five more occur also in the Eastern Pacific (Amphiamerican species). Endemic to the lower Caribbean are 106 species (40%), plus three Amphiamericans so far recorded only from the lower Caribbean (e.g., *Anachis varia*). Thirty-three species (12%) can be regarded

essentially as Antillean or West Indian, i.e., their distributions embrace predominantly the Antillean arc but overlap partially one or more of the subareas considered in the analysis. In contrast to this, six moderately widely distributed Caribbean species are exclusively bound to the continental shelves; i.e., their range does not include the Antillean arc (e.g., *Turbinella angulata*).

Although western Atlantic species are more or less homogeneously distributed among all subareas, making 61–70% of the total species, both lower Caribbean and “Antillean” species exhibit a tendency to concentrate in certain subareas (Fig. 2).

The families Costellariidae, Volutidae, Volutomitrididae, and Vexillidae obtained the lowest BGR's (their members tend to have narrow distributions), whereas Columbariidae, Colubrariidae, Melongenidae, Cypraeidae and Thaididae achieved the highest BGRs (the members of these families usually exhibited wide distributions).

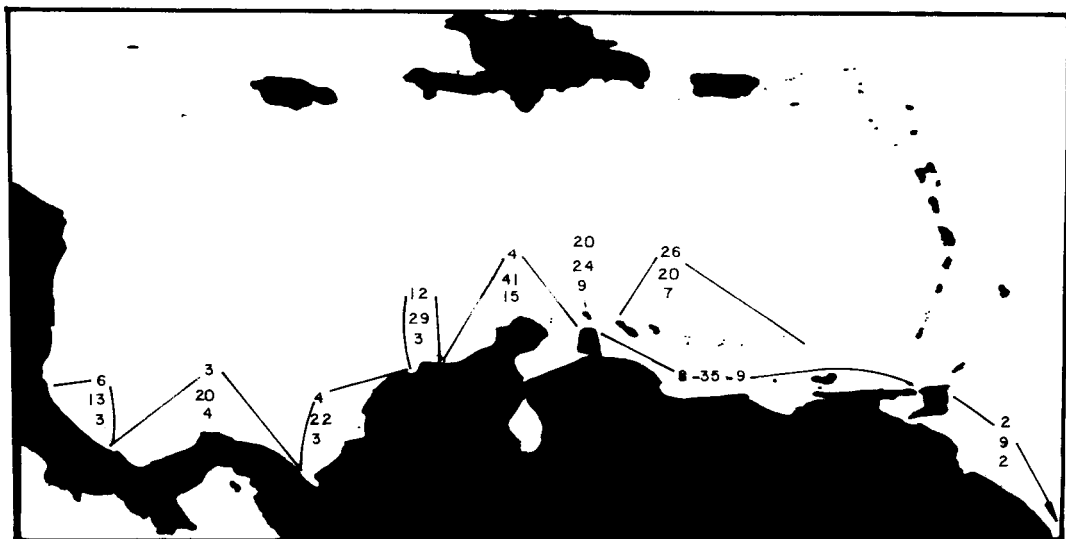


FIG. 2. Distribution of numbers of "Southern Caribbean" (upper number), "Antillean" (middle number), and exclusive (=endemic, lower or third number) species of higher gastropod among the subareas.

Average BGR of all species was 23.8; i.e., most species in the lower Caribbean exhibit a distribution range that encompasses slightly more than two of the nine subareas examined here.

Table 3 summarizes the number of species recorded and their average BGR, as well as shelf extent of the nine subareas. Clearly, the shelf extent of the subareas is not correlated with the number of species recorded. The subareas richest in species are V (47% of the total), M (45%), and A (44%). LI (42%) and G (41%) are slightly less diverse. In contrast, subareas R (31%) and O (19%) definitely have less diverse faunas.

The lowest average BGR was attained by the species recorded from G, followed by the species from LI and A. The highest values are achieved by species occurring in R, P, and C, whereas the species recorded from V and O attain moderate values.

Figure 3 shows subarea affinity based on untransformed presence-absence data, applying the conventional Czechanovsky measure of similarity and group-average sorting. A broken line at the arbitrary similarity level of 50% delineates two major groups of subareas (A-LI-V-M and C-P-R) and leaves subareas O and G detached.

The gastropod fauna of subarea O is the most dissimilar in the southern Caribbean. It is definitively impoverished, exhibits a very low endemism degree, and 53% of the species occurring there are wide-ranging in the Tropical Western Atlantic (53%). Although species endemic to the southern Caribbean are well represented (35.3%), the distribution area of several "Brazilian endemics" begins elsewhere between the Orinoco delta and French Guiana (e.g., *Tur-*

TABLE 3. Shelf extent, number of recorded species, and average Breath of Geographic Range (BGR) of the species recorded in the nine subareas analyzed.

Area	Shelf extent* (km) ²	Number of species	BGR average
Costa Rica (R)	4400	81	44.6
Panama (P)	26,000	101	43.3
Southern Colombia (C)	22,000	100	43.5
Santa Marta (M)	140	120	41.7
Goajira-Paraguaná (G)	45,000	108	31.6
Aruba (A)	250	117	35.7
Leeward Islands (LI)	2000	112	34.0
Central Venezuela (V)	65,000	124	37.6
Surinam-Guiana (O)	180,000	51	36.5

* Shelf width estimated from the shoreline to the 100 fathoms depth contour.

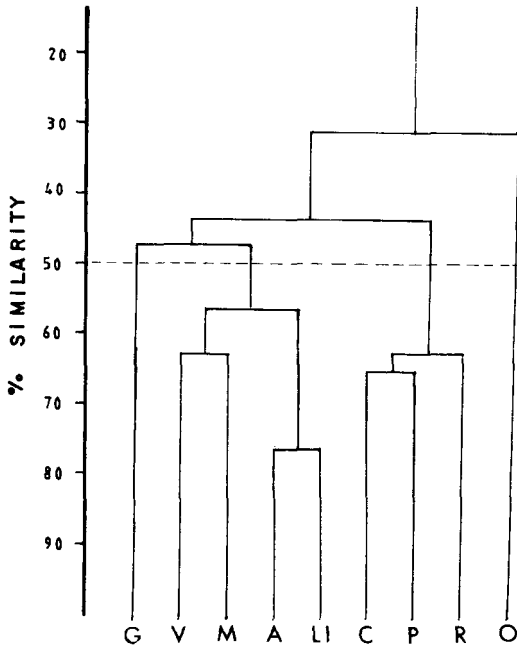


FIG. 3. Classification of nine subareas in the southern Caribbean based on presence-absence data of 266 gastropod species, using the Czechanovsky measure and group-average sorting. Two main groups of subareas and two detached subareas are distinguished at an arbitrary similarity level of 50%.

binella laevigata, *Marginella cloveri*). Zoogeographically, this subarea should be considered to be outside the Caribbean Sea.

Subareas V, M, A, and LI join together in the dendrogram (Fig. 3) forming a somewhat diffuse group characterized by a species-rich fauna. The close faunal affinity between Aruba and the remaining Leeward Islands off the Venezuelan coast is evident, in spite of the apparent environmental differences among both subareas. This resemblance is principally due to the relative high number of "Antillean" species occurring there. Of a total of 33 Antillean species "invading" the Lower Caribbean, 20 and 26 have been recorded respectively in subareas A and LI, making 17 and 22% of the whole caenogastropod fauna in these subareas ("Antillean" species yield only 4-10% of the gastropod fauna in the remaining subareas). The main difference between these two subareas results from a handful of endemics to one of them (nine species in A, seven in LI) and higher

incidence of sand-mud dwelling species in A (e.g., *Ficus communis*, *Antillophos candei*) versus a higher number of rock-coral dwelling gastropod in LI (e.g., *Pygmaepteris lourdesae*, *Dermomurex pauperculus*).

Subareas V and M share many wide ranging Tropical Western Atlantic and Lower Caribbean species, and some faunal elements apparently restricted to upwelling areas, i.e., occurring only in subareas M, G, and V (e.g., *Calotrophon velero*, *Fusinus caboblanquensis*). They also share several "Antillean" species, which are in part shared with subareas A and LI.

Subarea G is quite detached from the adjacent subareas. Almost half of the species endemic to the lower Caribbean occur there, many of them being restricted to it (15 species, or 14.7% of its caenogastropod fauna).

Subareas R, P, and C form a group having comparatively many wide-ranging species and a lower degree of endemism. Amphiamerican species are numerically concentrated in these subareas.

DISCUSSION

Concerning their habitat preferences, feeding habits, and sizes, the 266 species analyzed are diverse enough to be considered a representative sample of the prosobranch gastropod fauna in the region (cf. Rosenberg, 1993).

The duration of planktonic life has zoogeographic significance, since the dispersal capability of a species partially determines its range of distribution. Thus, gastropod species with direct development or whose larvae have short free-swimming stages show generally more restricted distribution than those with greater dispersal capability (Perron and Kohn, 1985; Scheltema, 1989). As stated above, average BGR was lowest among the families Costellariidae, Volutidae, Volutomitridae, and Vexillidae, all them with predominantly direct development (see Radwin and Chamberlain, 1973; Penchaszadeh, 1988). Single species of these families have very limited distribution within the Lower Caribbean, so that they are in part responsible for the incidence of endemism in certain subareas, such as G and P. On the other hand, av-

erage BGR's are high among families as Cypraeidae, Thaididae, Colubrariidae, and Melongenidae, which have mostly planktonic development (Radwin and Chamberlain, 1973; Bandel, 1976a).

Conversely, as one might expect from traditional island biogeographic theory (e.g., MacArthur and Wilson, 1967), the species-area effect alone offers little to explain why some of the analyzed subareas are currently species-richer than others.

As stated by Williamson (1988), the importance of environmental heterogeneity and historic biogeographic (antecedent) factors must be taken into account in evaluating biogeographic studies involving species-area relationships. In structurally diverse habitats, coexisting species often seem to specialize and to avoid competitive exclusion by differential use of the physical structure. Although it is difficult to evaluate all components of environmental heterogeneity and whether it is a cause or merely a correlate of species richness, it is possible to take the degree of co-occurrence of various shelf-bottoms types, water qualities, and habitats within a given subarea as a measure of its environmental heterogeneity. A coarse comparison of environmental features (Table 1) suggests a closer relationship with the total number of species recorded from each subarea than that resulting from consideration of shelf extent. Subareas R and O stand out clearly as the least environment-diverse and also the least species-rich.

The gastropod fauna of the southern Caribbean may be conveniently divided into four categories on the basis of their broad distribution patterns: (A) Species widely distributed in the Caribbean Sea or even in most parts of the tropical Western Atlantic (43% of the species); (B) amphiatlantic species (3%); (C) species restricted to the southern Caribbean, i.e., their whole range falls within the studied region (40%); and (D) Antillean species which extend into the southern Caribbean (12%).

Briggs (1974) subdivided the tropical Western Atlantic into three provinces according to his "10 percent-rule" (i.e., when 10% or more of the species are endemic to a given area, it is designated as a separate

province): Caribbean, West Indian, and Brazilian. According to this scheme, the studied area falls entirely within the "Caribbean Province," which extends along the continental coastline of Central and South America from Tampico (Mexico) to eastern Venezuela, including allopatrically the southern portion of the Florida Peninsula. Although the theoretical basis for the establishment of these provinces has been questioned (Voss, 1975), the scheme has been adopted by Caribbean zoogeographers (e.g., Spivey, 1981; González et al., 1991). Briggs' scheme contrasts with Petuch's statement (1982a, b) that the Caribbean Molluscan Province may be divided into northern and southern components by a line of abrupt faunal shift at about latitude 15°N. Further arguments in favor of a north-south faunal division of the Caribbean Region were provided by Acero (1985) on the basis of fish distribution patterns.

The data discussed in this paper show that the southern Caribbean harbors a gastropod fauna with 40% of endemism, enough to consider it a separate zoogeographic subregion. Nevertheless, Rosenberg (1993), by comparing gastropod lists of scattered and limited areas in the Western Atlantic, stated recently that no local region of the Western Atlantic has more than 4% endemics and subsequently no faunal province subdivisions could be made within this region. Since endemic species of a particular province or subprovince are not always restricted to a single locality or country, and similarities between local faunas are partly determined by habitat availability, in order to determine zoogeographic differences within a wide region faunal lists should be grouped first according to similarities among them and then one should examine similarities between the groups. In this way, groups of allied faunas are justly or better compared and actual differences between broad areas within the region become more evident.

The similarity analysis makes evident the faunal heterogeneity and variation among subareas within the southern Caribbean. A similarity level of 50% seems adequate to define biogeographic areas or subprov-

inces within the Southern Caribbean Province. Clearly, faunal shifts between adjacent subareas are not always sharply defined and the boundaries could be drawn anywhere, at least statistically. However, there may be valid ecological or zoogeographical reasons for locating the boundary in a certain place.

Subarea O (Fig. 1) should not be considered as a subprovince itself but as a transition area towards the Brazilian Province. The Orinoco delta is a zone of abrupt impoverishment of the Antillean-lower Caribbean fauna, whereas southwards from it a gradual enrichment of Brazilian elements takes place (cf. Rios, 1985; Cervigón et al., 1992).

Although subareas A and LI are both allied to M and V, the former exhibit about the same number of southern Caribbean and "Antillean" species (23 and 17% respectively in A; 19 and 22% in LI). Hence, the Leeward Islands should be regarded as a gradual transition area to the Antillean or West Indian Province, Aruba being the first step.

Subareas V and M represent a subprovince (I propose the name "Samaritan-Venezuelan Subprovince") that harbors the species-richest molluscan fauna in the southern Caribbean. It is seasonally affected by trade wind-induced upwelling of cold water (Bula-Meyer, 1977; Cervigón et al., 1992) and is disjuncted by subarea G, the latter being affected almost permanently by upwelling (Bula-Meyer, 1977; Corredor, 1979). Towards the east, this subprovince has a fairly well defined boundary at the eastern end of the Peninsula of Paria, coinciding with a coarse change in the environmental features (cf. Cervigón et al., 1992). On the other side, subarea M, representing the allopatric western portion, has a well defined faunal and environmental boundary to the south. An abrupt faunal shift at Santa Marta, caused possibly by the combined barrier effect of an extremely narrow shelf and upwelling-induced cold waters, has been documented (Cosel, 1976, 1982; Díaz and Götting, 1988; Díaz, 1990). The boundaries of this subprovince to subarea G are not so well defined (see below).

The shelf areas off La Goajira and Paraguaná and the Gulf of Venezuela (subarea G) are definitely a detached subprovince (I propose the name "Goajira Subprovince"). The uniqueness of the molluscan fauna of this area was first revealed by Petuch (1976), who announced subsequently the existence of a "Colombian-Venezuelan Neogene relict pocket holding the oldest known intact shallow water molluscan fauna in the Western Atlantic" (Petuch, 1981:311). The same author later described many of the former "living fossils" as new species (Petuch, 1987), some of which appear dubious because they were described from single specimens that may be only geographic varieties of wide-ranging species (cf. Díaz, 1990; Tursch and Huart, 1990). The boundaries of this subprovince are ill defined, but they can be conveniently set at the northern tip of the Paraguaná Peninsula (Cabo San Román) and near Palomino (about 60 km eastward from Santa Marta). This is coincidentally about the distribution range of *Syphocypraea mus* (cf. Petuch, 1979).

The "Isthmian Subprovince" embraces at least the coasts and shelf areas from near Ciénaga (Colombia) to the Costa Rica-Nicaragua boundary. It extends probably to northernmost Nicaragua (Cabo Gracias a Dios), where apparently a faunal shift takes place (cf. Petuch, 1982b; Acero, 1985). As pointed out by Cosel (1986), due to major river discharges most coastal and shelf areas in the southern Colombian Caribbean and Panama are characterized by muddy bottoms and turbid waters with lowered salinity. This could lead to the presence of another zoogeographically isolated area in the southern Caribbean. Evidence of the presence of this faunal pocket is the high number of mollusks, particularly bivalves, having sibling species in the eastern Pacific (Cosel, 1986). More recently, when describing some new gastropod from Panama, Petuch (1990) proposed the existence of a further relict pocket or faunule along the Caribbean coast of Panama and Costa Rica, the "Blasian Biogeographic Subregion," which, as shown above, encompasses also the southern part of the Colombian Caribbean.

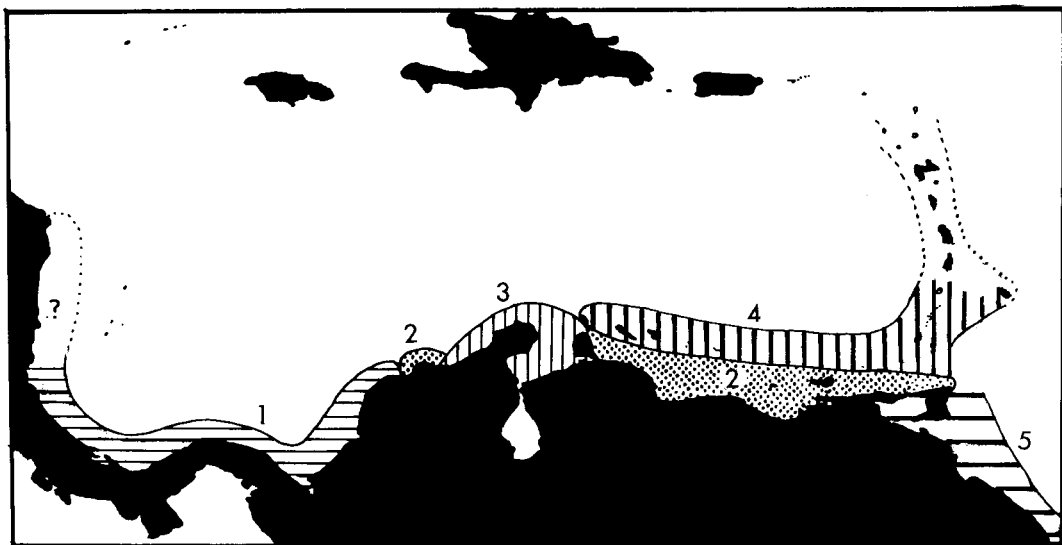


FIG. 4. Proposed spatial arrangement of molluscan subprovinces in the southern Caribbean: 1, Isthmian; 2, Samaritan-Venezuelan; 3, Goajira; 4, transition area to the Antillean province; 5, transition area towards the Brazilian province.

Figure 4 summarizes the spatial arrangement of molluscan subprovinces in the lower Caribbean as proposed above. The most plausible way to explain such zoogeographic schemes and faunal anomalies is to search for vicariant events that correspond to geological and paleoclimatic episodes of known age.

The fact that most species endemic to the southern Caribbean concentrate along the continental shelf of northern Colombia and Venezuela (Fig. 2) may be adequately explained from ecological factors causing vicariance. As pointed out by Petuch (1976), Meyer et al. (1978), and Vermeij (1978), the trade wind-induced upwelling of cold water along the coasts of Venezuela and northernmost Colombia may restrict to shallow water the distribution of many species of molluscs and crinoids of this region. The isolating "cold water" condition seems to have prevailed since the Tertiary as can be deduced from the existence of a Colombian-Venezuelan-Trinidad faunal subprovince during the Miocene (Woodring, 1974; Petuch, 1982a).

Shifts in oceanographic conditions after the Pliocene emergence of the Isthmus of Panama (Maier-Reimer et al., 1990), as well

as sea level fluctuations and changes in patterns of upwelling and nutrient distribution in northern South America during the Pleistocene (Jackson et al., 1993), caused not only high rates of extinction (Olsson, 1972; Vermeij, 1978; Vermeij and Petuch, 1986) but also high rates of speciation (Allmon et al., 1993; Jackson et al., 1993) and further disjunction of the molluscan fauna of that subprovince into three geographically discrete pockets, which are presently evidenced as a Goajira Subprovince and a disjoined Samaritan-Venezuelan Subprovince.

Likewise, the present Caribbean boundaries of the Isthmian Subprovince coincide with the Central American-northern South American Miocene faunal Subprovince (cf. Woodring, 1974). Many gastropod from the Plio-Pleistocene of Costa Rica also have a Holocene distribution in the western Caribbean, extending approximately from Honduras to Colombia (Robinson, 1993). The latter was disjoined by the final closing of the Isthmus of Panama and underwent drastic environmental changes during the Pleistocene, leading to the extinction of many molluscan genera and species in the Caribbean (Olsson, 1972; Petuch, 1982a;

Vermeij and Petuch, 1986). The present molluscan fauna of the Isthmian Subprovince is composed mainly of wide-ranging Western Atlantic or pan-Caribbean species. On the other hand, as the amount of endemic species is fairly low, it seems that the birth rate of new taxa in this subprovince has been lower than in the remaining subprovinces in the southern Caribbean. Hence, whereas the loss in diversity during the Pliocene and Pleistocene in many areas of the Western Atlantic was compensated for, mainly by speciation (Vermeij and Rosenberg, 1993), in the Isthmian Subprovince the loss was apparently compensated mostly by invading species which achieved wide distributions in the Western Atlantic (Vermeij and Rosenberg, 1993). Nevertheless, a significant amount of forms related to the Panamic fauna of Western Central and South America (amphiamerican and sibling species: 29% after Radwin, 1969; 17.5% after Kruckow, 1980; up to 58% after Cosel, 1986) underscore the zoogeographic links to the Panamic-Eastern Pacific.

Caenogastropod species distributions in the southern Caribbean suggest defined zoogeographic tendencies. They can be explained as a whole from a combination of historic biogeographic and dispersal factors, as well as regional environmental features. The proposed arrangement of gastropod distribution patterns in the lower Caribbean into three major discrete subprovinces should be further evaluated by workers studying other marine taxa.

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APPENDIX. Species considered for the analysis and subareas in the lower Caribbean where they have been recorded (R: Costa Rica; P: Panama; C: southern Caribbean coast of Colombia; M: Santa Marta; G: Goajira-Paraguana; V: northern Venezuela; A: Aruba; LI: Leeward Islands; O: Orinoco delta to Surinam).

Ficidae

- Ficus comunis* (Röding, 1798) G-V-A
F. howelli Clench & Aguayo, 1940 V-O

Muricidae

- Murex messorius* Sowerby, 1841 R-P-C-M-G-V-O
M. chrysostoma Sowerby, 1834 G-V-A-LI-O
M. olssoni Vokes, 1967 R-P-C-M-G
M. donmoorei Bullis, 1964 M-G-V-O
M. thompsoni Bullis, 1964 G-V-O
M. consuelae Verrill, 1950 M-LI
M. blakeanus Vokes, 1967 G-V
M. sunderlandi Petuch, 1987 G
M. tryoni Bullis, 1964 O
Chicoreus brevifrons (Lam., 1822) R-P-C-M-G-V-A-LI-O
C. spectrum (Reeve, 1846) A-LI
C. mergus Vokes, 1974 R
Phyllonotus pomum (Gmelin, 1791) R-P-C-M-V
P. margaritensis Abbott, 1958 G-V-A-LI
Siratus springeri Bullis, 1964 V-O
S. beauii Fischer & Bernardi, 1857 G-V-O
Paziella oregonia Bullis, 1964 G-V-O
Calotrophon nelero (Vokes, 1970) M-G-V-A-LI
Panamurex gatunensis (Brown & Pils., 1911) G-V
Actinotrophon actinophorus (Dan, 1889) P-C
Typhis expansus Sowerby, 1874 M-V-O
T. bullisi (Gertman, 1969) P-C-M-O
T. tytyrus Bayer, 1971 V
Pterotyphis pinnatus (Broderip, 1833) R-P-C-M-G
Risomurex withrowi Vokes & Houart, 1986 M-G-V-A-LI
R. cf. gilbertharrisi (Weisbord, 1962) G-V
R. deformis (Reeve, 1846) R-P-C
Muricopsis muricoides (C. B. Adams, 1845) R-P-M-V
M. oxytata (Smith, 1938) P-C-V-LI
M. praepauxillus (Maury, 1917) LI
M. huberti Radwin & D'Atilio, 1976 LI
Murexiella mcgintyi (Smith, 1938) A-LI
-

APPENDIX . Continued.

<i>M. edwardpauli</i> Petuch, 1990	P
<i>Favartia cellulosa</i> (Conrad, 1846)	C-M-V-A-LI-O
<i>F. alveata</i> (Kiener, 1842)	M-V-A-LI
<i>F. germaniae</i> (Vokes & D'Atillio, 1980)	LI
<i>Trachypollia nodulosa</i> (C. B. Adams, 1845)	R-P-C-M-V-A-LI
<i>T. didyma</i> (Schwengel, 1943)	P-M-V-A-LI-O
<i>Dermomurex pauperculus</i> (C. B. Adams, 1850)	R-P-M-LI
<i>D. kaicherae</i> Petuch, 1987	G
<i>D. alabastrum</i> (A. Adams, 1864)	R-P
<i>Pygmaepteris juanita</i> Gibson-Smith, 1980	M-V
<i>P. lourdesae</i> Gibson-Smith, 1980	M-LI
<i>Murexsul harasewyichi</i> Petuch, 1987	G
Columbariidae	
<i>Fulgurofusus brayi</i> (Clench, 1959)	P-C-G-V
Thaididae	
<i>Purpura patula</i> (L. 1758)	R-P-C-M-G-V-A-LI
<i>Thais deltoidea</i> (Lamarck, 1822)	R-P-C-M-V-A-LI
<i>T. rustics</i> (Lamarck, 1822)	R-P-C-M-V-A-LI
<i>T. haemastoma haemastoma</i> (L. 1767)	C
<i>T. haemastoma floridana</i> (Conrad, 1837)	R-P-C-V-A-LI
<i>T. coronata coronata</i> (Lamarck, 1822)	C-O
<i>T. coronata trinitatisensis</i> (Guppy, 1869)	P-C-M-V-O
Colubrariidae	
<i>Colubraria lanceolata</i> (Menke, 1828)	R-P-C-M-LI-O
<i>C. obscura</i> (Reeve, 1844)	P-C-M-A-LI
<i>C. swifti</i> (Tryon, 1881)	M-A
Melongenidae	
<i>Melongena melongena</i> L. 1758	R-P-C-M-G-V-A-LI-O
<i>Pugilina morio</i> L., 1758	V-O
Buccinidae	
<i>Bailya parva</i> (C. B. Adams, 1850)	R
<i>B. marijkae</i> Jong & Coomans, 1988	LI
<i>B. intricata</i> Dall, 1889	R-P
<i>Cantharus tinctus</i> (Conrad, 1846)	P-C-M-G-V-A-LI
<i>C. auritulus</i> (Link, 1807)	R-P-M-V-A-LI
<i>C. karinae</i> Usticke, 1959	M-G-V-A-LI
<i>Pisania pusio</i> (L., 1758)	R-P-C-M-G-V-A-LI
<i>Engina turbinella</i> (Kiener, 1835)	R-P-C-M-V-A-LI
<i>E. stootsi</i> Jong & Coomans, 1988	A
<i>E. demani</i> Jong & Coomans, 1988	A
<i>E. willemsae</i> Jong & Coomans, 1988	A
<i>Antillophos candei</i> (d'Orbigny, 1842)	R-C-M-G-V-A
<i>A. hazaliei</i> (Dautzenberg, 1900)	M-G-V
<i>A. cf. adelus</i> (Schwengel, 1942)	P-C-G
<i>Engoniophos uncinatus</i> (Say, 1826)	C-M-G-V-A-LI
<i>Metula agassizi</i> Clench & Aguayo	V
<i>M. linte</i> Guppy, 1882	R-P
<i>Mohnia kaicherae</i> Petuch, 1987	G
Columbellidae	
<i>Columbella mercatorial</i> (L., 1758)	R-P-C-M-G-V-A-LI
<i>Minipirene dormitor</i> (Sowerby, 1844)	V-A-LI
<i>Conlla ovulata</i> (Lamarck, 1822)	R-P-V-A-LI

APPENDIX. Continued.

<i>C. ovuloides</i> (C. B. Adams, 1850)	P-A-LI
<i>Anachis obesa</i> (C. B. Adams, 1845)	R-P-C-M-G-V-A-O
<i>A. lyrata</i> (Sowerby, 1832)	R-P-C-M-G
<i>A. coseli</i> Díaz & Mittnacht, 1990	C-M-G
<i>A. cf. fraudans</i> Jung, 1969	M-G
<i>A. hotessieriana</i> (d'Orbigny, 1842)	M-LI
<i>A. demani</i> Jong & Coomans, 1988	A
<i>A. sparsa</i> (Reeve, 1859)	R-P-C-M-G-V-A-LI
<i>A. catenata</i> (Sowerby, 1844)	R-P
<i>A. sertulariarum</i> (d'Orbigny, 1839)	C-M-G-V-O
<i>A. pretri</i> (Duclos, 1846)	P-M-V-A-LI
<i>A. pulchella</i> (Blainville, 1829)	R-P-C-M-V-A-LI
<i>A. dicomata</i> Dall, 1899	A-LI
<i>A. varia</i> (Sowerby, 1832)	R-P-C
<i>A. plicatula</i> (Dunker, 1853)	V-A-LI
<i>Cosmiococoncha nitens</i> (C. B. Adams, 1845)	P-G-V
<i>C. calliglypta</i> (Dall & Simpson, 1901)	C-M-O
<i>C. hurmfreyi</i> Jong & Coomans, 1988	A
<i>Mitrella ocellata</i> (Gmelin, 1791)	R-P-C-M-G-V-A-LI
<i>M. lunata</i> (Say, 1826)	R-P-C-M-G-A-LI-O
<i>M. nycteis</i> (Duclos, 1846)	P-M-A-LI
<i>M. dichroa</i> (Sowerby, 1844)	P-C-M-V-LI
<i>M. idalina</i> (Duclos, 1840)	A-LI
<i>Nitidella nitida</i> (Lamarck, 1822)	R-P-C-M-G-V-A-LI
<i>N. laevigata</i> (L., 1758)	R-P-C-M-G-V-A-LI
<i>Decipifus sixaolus</i> Olsson & McGinty, 1958	P-M-G-V-A-LI
<i>D. kirstenseni</i> Jong & Coomans, 1988	LI
<i>Mazatlaniania aciculata</i> (Lamarck, 1822)	R-P-C-M-V
<i>Strombina pumilio</i> (Reeve, 1859)	G-V
<i>S. francesae</i> Gibson-Smith, 1974	V
Fasciolariiidae	
<i>Fasciolaria tulips</i> (L., 1758)	R-P-C-M-G-V-A-LI
<i>Latirus infundibulum</i> (Gmelin, 1791)	P-C-M-G-V-A-LI-O
<i>L. mcgintyi</i> Pilsbry, 1939	P-C-M-G-LI
<i>L. cariniferus</i> (Lamarck, 1822)	R-P
<i>L. angulatus</i> (Röding, 1798)	M-V-A-LI
<i>L. eppi</i> Melvill & Shepman, 1891	LI
<i>Teralatirus ernesti</i> (Melvill, 1910)	A-LI
<i>T. cayohuesonicus</i> (Sowerby, 1878)	P-C-M-V-A-LI
<i>Dolicholatirus pauli</i> (McGinty, 1955)	M
<i>Leucozonia nassa</i> (Gmelin, 1791)	R-P-C-M-G-V-A-LI
<i>L. ocellata</i> (Gmelin, 1791)	R-P-C-M-V-A-LI
<i>Fusinus closter</i> (Philippi, 1850)	M-G-V-A-O
<i>F. couei</i> Petit, 1853	V
<i>F. helenae</i> Bartsch, 1939	G-V
<i>F. caboblanquensis</i> Weisbord, 1964	M-G-V
<i>F. eucosmius</i> (Dall, 1889)	O
<i>Harasewyichia harasewyichi</i> Petuch, 1987	G
Volutilidae	
<i>Voluta musics</i> L., 1758	M-G-V-A-LI
<i>V. uirescens</i> (Lightfoot, 1786)	R-P-C
<i>V. demarcoi</i> Olsson, 1965	R
<i>V. lacertina</i> Petuch, 1990	P
<i>Scaphella evelina</i> Bayer, 1971	C
<i>Volutomitra erebus</i> Bayer, 1971	G

APPENDIX . Continued.

<i>V. persephone</i> Bayer, 1971	P-G-V
<i>Lyria leonardi</i> Emerson, 1985	v
Harpidae	
<i>Morum oniscus</i> (L., 1767)	R-C-M-V-A
<i>Cancellomorum lindae</i> (Petuch, 1987)	G
Cancellaridae	
<i>Cancellaria reticulate</i> (L., 1767)	R-C-M-G-V-O
<i>Agatrix srnithi</i> (Dall, 1888)	M-V
<i>Aphera lindae</i> Petuch, 1987	V
Turbinellidae	
<i>Turbinella angulata</i> (Lightfoot, 1786)	R-P-C-M-G
<i>T. laevigata</i> Anton	O
Vasidae	
<i>Vasum muricatum</i> (Born, 1778)	R-P-C-M-G-V-A
<i>V. capitellum</i> (L., 1758)	V-A-LI
Olividae	
<i>Oliva oblongs</i> Marrat, 1871	M-G-V-A
<i>O. bewleyi</i> Marrat, 1871	P-C
<i>O. reticularis</i> Lamarck, 1810	R-A-LI
<i>O. scripts</i> Lamarck, 1810	R-P-C-M-V-
<i>O. fulgurator</i> Rödiger , 1798	V-A
<i>O. circinata</i> Marrat, 1871	G
<i>O. reclusa</i> Marrat, 1871	A
<i>O. goajira</i> Petuch & Sargent, 1987	G
<i>Olivella olssoni</i> Altena, 1975	C-M-G-O
<i>O. minuta</i> (Link, 1807)	R-P-C-M-G-V-A-LI-O
<i>O. myrmecoon</i> Dall, 1912	R-P-C-M-G
<i>O. ankei</i> Diaz & Götting , 1989	M-A-LI
<i>O. nivea</i> (Gmelin, 1791)	P-C-M-V-A-O
<i>O. dealbata</i> (Reeve, 1850)	LI
<i>O. lactea</i> (Marrat, 1871)	C-M-O
<i>O. petiolita</i> (Duclos)	P-V
<i>O. floralia</i> (Duclos, 1853)	M-A-LI
<i>Jaspidella blanesi</i> (Ford, 1898)	P-C-M-V
<i>J. jaspidea</i> (Gmelin, 1791)	P-C-V-A-LI
<i>Ancilla glabrata</i> (L., 1758)	M-G-V-A
<i>A. bulteata</i> (Sowerby, 1823)	A
<i>A. lienardi</i> (Bernardi, 1858)	A
<i>A. tankervillei</i> (Swainson, 1825)	V
<i>Agaronia testacea</i> (Lamarck)	R-P
Marginellidae	
<i>Prunum prunum</i> (Gmelin, 1791)	C-M-G-V-LI-O
<i>P. cf. rostratum</i> Redfield	M
<i>P. labiatum</i> Kiener	P-C
<i>P. apicinum</i> (Menke, 1828)	R-A
<i>P. marginatum</i> (Born, 1778)	M-G-V-A-LI-O
<i>P. guttatum</i> (Dillwyn, 1817)	P-C
<i>Marginella carnea</i> Storer, 1837	P
<i>M. margarita</i> (Kiener, 1834)	LI
<i>M. cloveri</i> Rios & Matthews, 1972	O
<i>Dentimargo aureocincta</i> Stearns, 1872	P-C
<i>D. reducta</i> (Bavay, 1922)	C-M-G-V-A

APPENDIX. Continued.

<i>D. sulcata</i> (d'Orbigny, 1842)	C-A-LI
<i>D. eburneola</i> (Conrad, 1834)	R
<i>Marginellopsis serrei</i> Bavay, 1911	A-LI
<i>Persicula muralis</i> (Hinds, 1844)	V-A-LI
<i>P. interruptolineata</i> (Mühlfeldt, 1816)	C-M-G-V-A-LI
<i>P. maculosa</i> (Kiener, 1834)	V-A
<i>P. cordorae</i> Jong & Coomans, 1988	LI
<i>P. porcellana</i> (Gmelin, 1791)	C
<i>P. fluctuata</i> (C. B. Adams, 1850)	R-M
<i>P. pulcherrima</i> (Gaskoin, 1849)	M-G-V-A-LI
<i>P. catenata</i> (Montagu, 1803)	P-A-LI
<i>P. chrysomelina</i> (Redfield, 1848)	A-LI
<i>P. weberi</i> Olsson & McGinty, 1958	R-P
<i>Pachybatron tayrona</i> Díaz & Vel., 1987	M
<i>P. cypraeoides</i> (C. B. Adams, 1845)	A-LI
<i>Cysticus jansseni</i> Jong & Coomans, 1988	M-G-LI
<i>Volvarina avena</i> (Kiener, 1834)	R-P-C-M-G-V-A-LI
<i>Cypraeolina ovuliformis</i> (d'Orbigny, 1841)	P-C-M-G-V-A-LI
<i>C. antillensis</i> Jong & Coomans, 1988	LI
Mitridae	
<i>Mitra nodulosa</i> (Gmelin, 1791)	R-P-C-M-V-A
<i>M. barbadensis</i> (Gmelin, 1791)	R-P-C-V-A-LI-O
<i>M. leonardi</i> Petuch, 1990	P
<i>Pusiolina veldhoveni</i> Jong & Coomans, 1988	M-A-LI
<i>Pusia puella</i> (Reeve, 1845)	P-M-A-LI
<i>P. pulchella</i> (Reeve, 1844)	V-A
<i>P. exigua</i> (C. B. Adams, 1845)	R-P-M-V-A-LI
<i>P. venusta</i> Sarasua, 1978	M
<i>P. cubana</i> Aguayo & Rehder, 1936	M
<i>P. dermestina</i> (Lamarck, 1811)	R-P-M-V-A-LI
<i>P. variata</i> (Reeve, 1845)	R-A
<i>P. histrio</i> (Reeve, 1844)	P-A-LI
<i>P. sykesi</i> (Melvill, 1925)	R-A-LI
<i>P. monilifera</i> (C. B. Adams, 1845)	P-C-M-V-A-LI
<i>P. hendersoni</i> (Dall, 1927)	O
<i>P. laterculata</i> (Sowerby, 1874)	R-C-M-A-LI
<i>P. bibsae</i> (Usticke, 1969)	A
<i>P. epiphaneum</i> (Rehder, 1943)	R
<i>Subcancilla leonardhilli</i> Petuch, 1987	M-G-V
<i>Conomitra lindae</i> Petuch, 1987	G
<i>C. caribbeana</i> Weisbord, 1929	V
<i>Turricostellaria lindae</i> Petuch, 1987	G-V
<i>T. leonardhilli</i> Petuch, 1987	G
<i>Nodicostellaria kremerae</i> Petuch, 1987	G
Conidae	
<i>Conus ermineus</i> Born, 1778	R-M-G-A-LI-O
<i>C. spurius</i> Gmelin, 1791	P-C-M-G-V-A
<i>C. spurius lorenzianus</i> Dillwyn, 1817	R-P-C
<i>C. mus</i> Hwass, 1792	R-P-C-M-G-A-LI
<i>C. jaspideus</i> Gmelin, 1791	P-C-M-G-V-A-LI-O
<i>C. puncticulatus</i> Hwass, 1792	R-C-M-G-V-A-LI
<i>C. mappa granarius</i> Kiener, 1848	M-G
<i>C. mappa trinitarius</i> Hawass, 1792	V
<i>C. regius</i> Hwass, 1792	R-P-C-M-A-LI

APPENDIX. Continued.

<i>C. daucus</i> Hwass, 1792	R-P-M-A-LI-O
<i>C. penchaszadehi</i> Petuch, 1986	M-G
<i>C. centurio</i> Born, 1778	M-G-A-LI-O
<i>C. brunneofilaris</i> Petuch, 1990	P
<i>C. amphiurgus</i> Dall, 1889	C-M
<i>C. kevani</i> Petuch, 1987	G
<i>C. austini</i> Rehder & Abbott, 1951	M-G-V-O
<i>C. cingulatus</i> Lamarck, 1810	P-C-M
<i>C. forsteri</i> Clench & Aguayo, 1942	V-O
<i>C. bayeri</i> Petuch, 1987	C
<i>C. mindanus</i> Hwass, 1792	P-A-LI
<i>C. granulates</i> L., 1758	R-P-C-LI
<i>C. hieroglyphus</i> Duclos, 1833	A-LI
<i>C. curassaviensis</i> Hwass, 1792	A
<i>C. aurantius</i> Hwass, 1792	LI
<i>C. attenuates</i> Reeve, 1844	LI
<i>C. parascalaris</i> Petuch, 1987	G
<i>C. perprotractus</i> Petuch, 1987	G
Terebridae	
<i>Terebra weisbordi</i> Gibson-Smith, 1984	C-M-G-V
<i>T. trispiralis</i> Weisbord, 1964	V
<i>T. protexta</i> Conrad	P-C-M-G-V-A-LI
<i>T. salleana</i> (Born, 1778)	R-P-C-M-G-V-A-O
<i>T. dislocata</i> (Say, 1822)	R-P
<i>T. curacaoensis</i> Jong & Coomans, 1988	A-LI
<i>T. hastata</i> (Gmelin, 1791)	P-C-M-G-V-A-LI-O
<i>T. taurina</i> (Lightfoot, 1786)	P-C-M-G-V-A-LI-O
