

GEOGRAPHIC AND HABITAT-SPECIFIC MORPHOLOGICAL VARIATION OF
LITTORARIA (LITTORINOPSIS) ANGULIFERA (LAMARCK, 1822)

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ABSTRACT

Recent, detailed examination of the morphology of the Littorinidae inhabiting Indo-West Pacific mangrove forests led Reid (1986) to identify 20 species of *Littoraria*, all of which had previously been assigned to only three species within the pantropical "*Littorina scabra*." No similar study has been done on the neotropical *Littoraria angulifera* (Lamarck), which occurs in mangrove forests on both sides of the Atlantic Ocean. We quantified variability in shell and genital morphology of *L. angulifera* throughout its range in the tropical Atlantic using material from both museum collections and new, field collections. We tested two hypotheses regarding variation in shell shape and sculpture, and frequency of color morphs in populations of *L. angulifera*: (1) observed variation is associated with the five major current regimes that could restrict its dispersal throughout the tropical Atlantic; or (2) observed variation is associated with habitat characteristics that can influence shell thermal properties. Strong geographical variation in shell shape and sculptural characteristics suggested initial support for the dispersal hypothesis. Absence of geographical variation in genital morphology, however, led to the rejection of the dispersal hypothesis. Parallel associations of habitat with geography suggests that *L. angulifera* is a single species throughout the tropical Atlantic, and observed variability results primarily from responses to local environmental conditions. However, this conclusion can be tested only with additional genetic analysis of disparate populations of *L. angulifera*.

Key words: Atlantic, currents, *Littoraria angulifera*, Littorinidae, mangroves, morphology, shell sculpture, shell shape.

INTRODUCTION

A recent, detailed examination of the morphology of the Littorinidae inhabiting Indo-West Pacific mangrove forests by Reid (1986, 1989, 1999) resulted in the identification of 21 species, all of which had previously been assigned to only three species within the pantropical "*Littorina scabra*" complex by Rosewater (1970, 1980). Reid (1986) also re-assigned these mangrove-inhabiting littorinids to the genus *Littoraria* Griffith & Pidgeon. No similar study has been done on the neotropical species *Littoraria angulifera* (Lamarck), which occurs in mangrove forests on both sides of the Atlantic Ocean, although Reid (1986, 1989) considered Eastern and Western Atlantic populations of *L. angulifera* to be a single species based on shell morphology and genital characteristics. Rosewater (1980) considered the neotropical "*Littorina angulifera*" to be a subspecies of "*Littorina scabra*," although

earlier authorities (e.g., Bequaert, 1943; Marcus & Marcus, 1964; Bandel, 1974) conferred distinct species status on *L. angulifera*, principally because of its geographical isolation from the Indo-West Pacific. Like its Indo-West Pacific congeners, *L. angulifera* is variable in shell morphology and color, and we studied this variability with respect to geography, potential dispersal routes, and habitat characteristics in the tropical Atlantic. In particular, we used museum collections and new field-collected material to test between two hypothesis that could account for observed variation in shell shape and sculpture, and frequency of color morphs in populations of *L. angulifera*. First, such variation could be associated with the five major current regimes that could restrict its dispersal throughout the tropical Atlantic. Alternatively, observed variation could be a consequence of habitat characteristics that can influence shell morphology and attendant thermal properties. We also use these

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data to discuss the need for further field studies and systematic re-evaluation of *L. angulifera* throughout its range.

Intraspecific variation in shell morphology of littorinids has been attributed both to environmental influences and genetic variability (Berry, 1961; Newkirk & Doyle, 1975; Janson, 1982a, b; Cook et al., 1985; Cook, 1992; Cook & Garbett, 1992; Lewis & Williams, 1995; Mill & Grahame, 1995). For example, supratidal and high intertidal snails subject to dessication stress tend to be highly ornamented or grooved (Vermeij, 1973). Smaller, more globose shells tend to occur in high-intertidal populations subject to frequent, high-intensity waves, while high-spired shells tend to be found in more protected areas (North, 1954; Newkirk & Doyle, 1975; Roberts & Hughes, 1980; Janson, 1982b; Johannesson, 1986; Brown & Quinn, 1988; Boulding & Van Alstyne, 1993; Lewis & Williams, 1995; Johannesson et al., 1997). Snails in low-density populations where food is abundant grow faster and tend to have rounder (low-spired) shells (Berry, 1961; Kemp & Bertness, 1984). By contrast, *Littorina subrotundata* Carpenter produces taller shells when it grows rapidly (Boulding & Hay, 1993). High levels of predation are associated with increased sculpturing (e.g., nodules and spines) and shell thickening (Reimchen, 1979, 1982; Cook, 1983; Reid, 1992; Cook & Kenyon 1993). These patterns have been documented primarily in the temperate zone, however. In contrast, studies of tropical littorines have been focused primarily on systematics (Bequaert, 1943; Rosewater, 1970, 1972; Reid, 1986, 1989), zonation (Sasekumar, 1974; Reid, 1985), predation (Reid, 1992), and intraspecific shell-color polymorphisms (Reimchen, 1979; Cook, 1983; Cook & Freeman 1986; Reid, 1987; Cook & Kenyon, 1993) of Indo-Pacific species. Little attention has been paid to intraspecific morphological variability of littorinids of the tropical Atlantic since the studies of Vermeij (1974), Borkowski (1975), and Rosewater (1981), which predate Reid's re-evaluation of the genus *Littoraria*.

Here, we document extensive morphological variability in *L. angulifera* from both sides of the Atlantic Ocean. *Littoraria angulifera* is one of only two littorinids known to occur on both sides of the Atlantic (Rosewater & Vermeij, 1972) (Fig. 1), and as such is an exemplar with which to address questions of geographically based intraspecific morphological variability. Because five distinct oceanic cur-

rents occur within the range of *L. angulifera*, we expected to see regional divergence in morphology that could indicate geographically defined subpopulations based on restricted larval dispersal. In addition, the significant variation in mangrove forest structure and nutrient availability that occurs throughout the tropical Atlantic also could contribute to variability in morphology. Morphological variation caused by local environmental characteristics could either amplify or mask morphological variation of some traits due to geographic isolation. Thus, we explore how several morphological characteristics covary with geography and features of local habitats.

MATERIALS AND METHODS

Natural History and Morphology

Littoraria (Littorinopsis) angulifera (Fig. 2) is the only tropical littorinid that is found exclusively in mangrove swamps of the Atlantic and Caribbean (see distribution map in Rosewater & Vermeij, 1972). *Littoraria angulifera* is ovoviviparous, with a planktotrophic larval stage estimated to be 8–10 weeks long (Gallagher & Reid, 1979). Adult snails occur in the supralittoral zone on trunks, roots, stems, and leaves of mangroves, primarily *Rhizophora mangle* L., *Avicennia* spp., and *Laguncularia racemosa* (L.) Gaertn.f., where they feeds on epiphytic algae and marine fungi (Kohlmeyer & Bebout, 1986). Because of its supralittoral habit, local variation in wave strength and exposure is unlikely to affect *L. angulifera*. Predation on *L. angulifera* has not been studied, although omnivorous grapsid crabs and predatory wading birds (egrets, herons) are often seen feeding in and around mangrove roots at low tide (A. M. Ellison, personal observation).

The normally light-orange protoconch is characterized by 3–5 prominent spiral ridges running parallel to the 2–4 whorls. Primary grooves appear on the 1st–4th whorl of the teleoconch, along with the axial striae (growth lines), which do not appear to conform to any spatial pattern on the shell surface (Fig. 3). Beginning between the 3rd and last whorls of the teleoconch, secondary grooves bisect the ribs between already existing primary grooves (Fig. 3). When present, tertiary grooves, like secondary grooves, appear on the ribs between already existing grooves (Fig. 3). If they

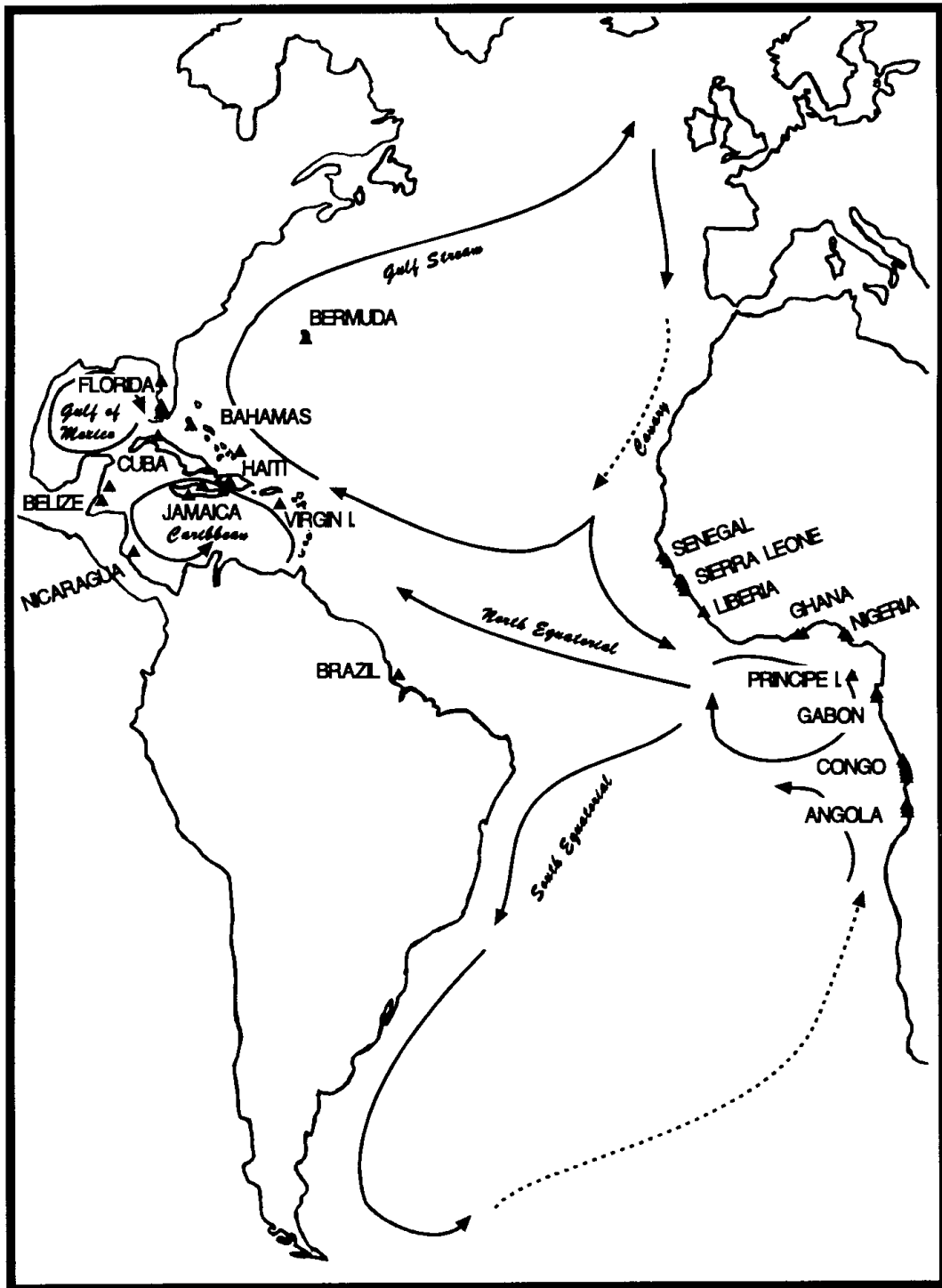


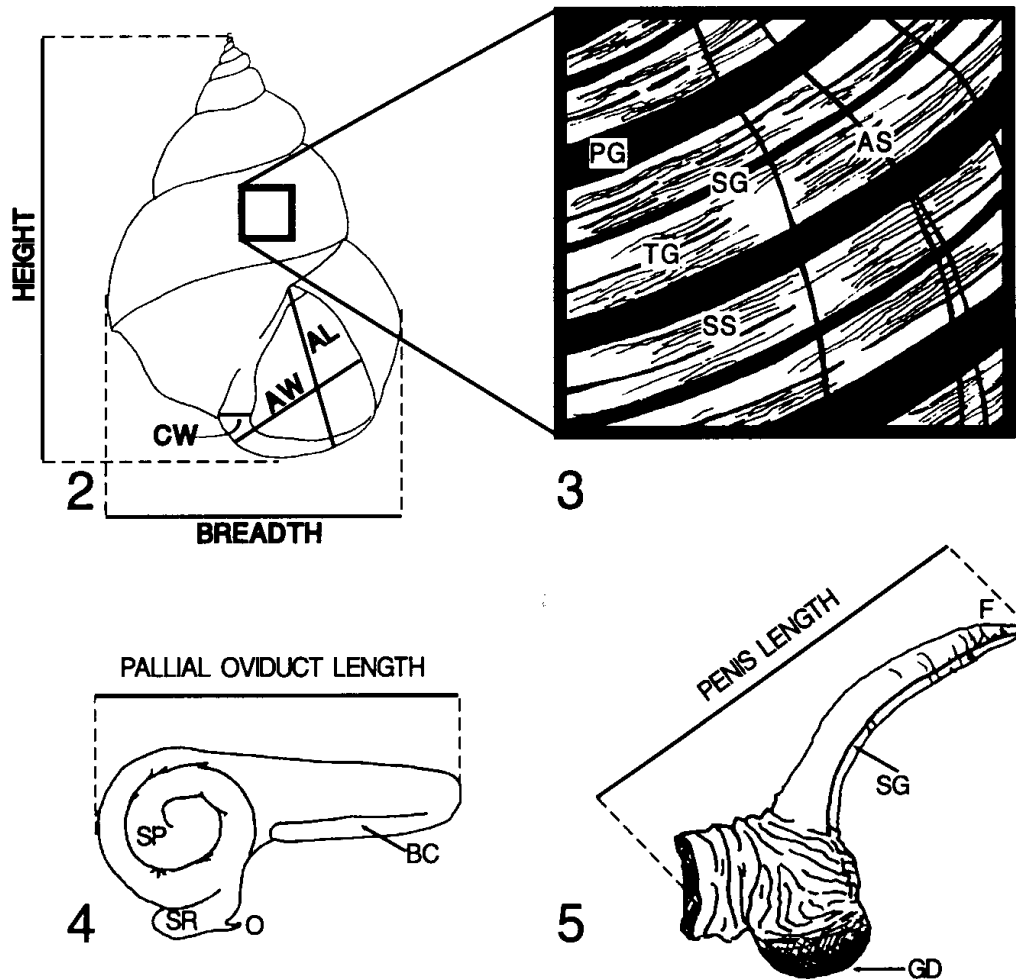
FIG. 1. Map illustrating collection localities of *Littoraria angulifera* and the prevailing currents in the Atlantic Ocean. Solid arrows are warm currents and dotted arrows are cold currents.

occur, spiral striae typically begin between the 4th and last whorls of the teleoconch (Fig. 3).

Samples and Measurements

We followed methods of Reid (1986) in collecting morphological data. A total of 1,042

specimens were examined from 41 sites throughout the distribution of *L. angulifera* (Table 1). The sample size from any single location ranged from two specimens to >100. The collections of the Academy of Natural Sciences in Philadelphia, Pennsylvania (ANSP) and The Natural History Museum, London



FIGS. 2–5. Shell shape and sculpture, and genitalia. 2. Illustration of measurements taken on an individual shell. CW: Columellar width; AW: Aperture width; AL: Aperture length. 3. Inset showing shell sculpture. PG: Primary groove; SG: Secondary groove; TG: Tertiary groove; AS: Axial stria; SS: Spirial striae. 4. Pallial oviduct. SP: Spiral loop; BC: Bursa copulatrix; SR: Seminal receptacle; O: Oviduct. 5. Penis. F: Filament; SG: Sperm groove; GD: Glandular disc.

(BMNH), were examined along with snails that we or our colleagues collected in 1996 in Florida, Belize, and Jamaica (vouchered at BMNH; Registration numbers 1996411 through 1996416). In most cases, only shells were available for study, but when preserved material was available (Florida, Belize, Jamaica, Sierra Leone, Ghana), samples were dissected and examined for comparison of anatomical characteristics as well. Dissected specimens were preserved in formalin and exhibited a certain degree of shrinkage, contortion, and discoloration. This made it impossible to identify finer characteristics, such as gamete structure and head-foot coloration. *Littoraria angulifera* secondarily has lost its egg capsule glands (Reid, 1986), so we could not use characters associated with them.

Categories of shell characteristics studied

included shape, appearance, sculpture, and color (when possible) (Figs. 2, 3). The shape of *L. angulifera* shells is typical of ovoviviparous, mangrove-dwelling littorines, with a high spire and an almost circular aperture (Reid, 1986). Five measurements—height, breadth, apertural width and length, and columellar width—were taken on each shell (Fig. 2) using calipers (± 0.1 mm). Four of these measurements were collapsed into three standard composite variables: proportionality (= height/breadth), circularity (= apertural width/apertural length), and spire height (= height/apertural length).

Sculpture characteristics (Fig. 3, Table 2) were identified using a dissecting microscope. The central columella of *L. angulifera* tends to be creamy yellow in color, convex and pinched at its base, with excavation of the

TABLE 1. Collection locations (in bold) and sites (in normal font), sample source, geographic coordinates (approximate latitude, longitude), current grouping to which we assigned each location, and shell shape characteristics for all sites studies. Values given are means, with 1 SD in parentheses. Grand means for each of the 19 locations are printed in boldface type, while means for sites within locations (where there are multiple sites within a location) are printed in normal type.

Location (Site)	Source ¹	Coordinates	Current grouping	Proportionality	Circularity	Spire Height
Angola		14° E, 8° S	South Equatorial	1.36 (0.047)	0.76 (0.036)	1.69 (0.059)
St. Paul de Loanda	ANSP			1.37 (0.052)	0.77 (0.030)	1.67 (0.043)
Loanda	BMNH			1.39 (0.018)	0.71 (0.015)	1.81 (0.071)
Cazangai	BMNH			1.33 (0.030)	0.74 (0.032)	1.69 (0.053)
Bahamas		78° W, 27° N	Gulf Stream	1.51 (0.091)	0.76 (0.026)	1.86 (0.078)
Great Abaco Island	ANSP			1.55 (0.089)	0.76 (0.023)	1.86 (0.079)
Little San Salvador Island	ANSP			1.46 (0.065)	0.75 (0.034)	1.87 (0.081)
Belize		88° W, 17° N	Caribbean	1.42 (0.060)	0.76 (0.029)	1.85 (0.080)
Garbutt Cay	ANSP			1.47 (0.061)	0.79 (0.030)	1.84 (0.060)
Wee Wee Cay	Elison			1.41 (0.056)	0.76 (0.026)	1.85 (0.083)
Bermuda		65° W, 33° N	Gulf Stream	1.53 (0.063)	0.77 (0.013)	1.87 (0.112)
ANSP				1.43 (0.071)	0.74 (0.031)	1.71 (0.050)
Brazil		50° W, 0° N	North Equatorial	1.43 (0.071)	0.74 (0.031)	1.71 (0.050)
ANSP				1.39 (0.072)	0.79 (0.047)	1.71 (0.112)
Congo		15° E, 6° S	South Equatorial	1.39 (0.072)	0.79 (0.047)	1.71 (0.112)
Banana (I)	ANSP			1.41 (0.075)	0.81 (0.063)	1.76 (0.135)
Banana (II)	ANSP			1.42 (0.049)	0.78 (0.032)	1.71 (0.093)
Banana Creek	ANSP			1.38 (0.066)	0.79 (0.026)	1.64 (0.078)
Port Gentil	ANSP			1.28 (0.042)	0.85 (0.007)	1.69 (0.142)
Kongo Town	BMNH			1.35 (0.083)	0.78 (0.021)	1.76 (0.123)
Banana (III)	ANSP			1.33 (0.052)	0.75 (0.033)	1.68 (0.090)
Cuba		85° W, 23° N	Caribbean	1.48 (0.062)	0.78 (0.034)	1.89 (0.108)
ANSP				1.45 (0.125)	0.74 (0.032)	1.86 (0.082)
Florida		82° W, 27° N	Gulf of Mexico	1.45 (0.125)	0.74 (0.032)	1.86 (0.082)
Little Shark River (middle)	Elison			1.57 (0.203)	0.74 (0.032)	1.87 (0.079)
Little Shark River (upper)	Elison			1.42 (0.053)	0.73 (0.026)	1.85 (0.070)
Little Shark River (mouth)	Elison			1.41 (0.058)	0.74 (0.042)	1.83 (0.076)
Cockroach Bay	Elison			1.38 (0.050)	0.74 (0.029)	1.81 (0.078)
Hurricane Island	Elison			1.47 (0.056)	0.75 (0.022)	1.95 (0.066)

(continued)

TABLE 1. (Continued)

Location (Site)	Source ¹	Coordinates	Current grouping	Proportionality	Circularity	Spire Height
Gabon						
Gabon Coast	BMNH	10° E, 2° S	South Equatorial	1.39 (0.053)	0.76 (0.040)	1.74 (0.114)
"West Africa"	BMNH			1.37 (0.069)	0.80 (0.024)	1.64 (0.086)
Ghana						
Gold Coast	BMNH	2° W, 5° N	North Equatorial	1.40 (0.040)	0.74 (0.030)	1.80 (0.079)
"Ghana"	BMNH			1.37 (0.046)	0.71 (0.041)	1.74 (0.089)
Haiti						
Gold Coast	BMNH			1.29 (0.025)	0.73 (0.010)	1.57 (0.043)
"Ghana"	BMNH			1.38 (0.043)	0.71 (0.042)	1.74 (0.083)
Jamaica	ANSP	74° W, 18° N	Gulf Stream	1.49 (0.094)	0.76 (0.017)	1.89 (0.112)
Great Goat Island	ANSP	78° W, 17° N	Caribbean	1.45 (0.083)	0.76 (0.035)	1.84 (0.085)
St. Anne's Bay	Nemeth			1.53 (0.090)	0.79 (0.033)	1.79 (0.088)
Liberia						
Great Goat Island	BMNH	10° W, 7° N	North Equatorial	1.42 (0.053)	0.75 (0.025)	1.86 (0.074)
St. Anne's Bay	ANSP			1.36 (0.007)	0.74 (0.007)	1.69 (0.023)
Nicaragua						
Lagos Lagoon	BMNH	85° W, 13° N	Caribbean	1.48 (0.044)	0.74 (0.020)	1.69 (0.023)
Lagos	ANSP	5° E, 5° N	North Equatorial	1.33 (0.030)	0.74 (0.053)	1.66 (0.079)
Nigeria						
Lagos Lagoon	BMNH			1.32 (0.018)	0.77 (0.039)	1.69 (0.060)
Lagos	BMNH			1.33 (0.035)	0.73 (0.057)	1.65 (0.087)
Principe Island	BMNH	8° E, 3° N	North Equatorial	1.30 (0.055)	0.78 (0.082)	1.64 (0.087)
Senegal						
"Senegal" (I)	BMNH	16° W, 13° N	North Equatorial	1.54 (0.373)	0.75 (0.034)	1.79 (0.080)
"Senegal" (II)	BMNH			1.46 (0.070)	0.74 (0.035)	1.85 (0.093)
Solomon (Senegambia)	BMNH			1.62 (0.504)	0.76 (0.039)	1.75 (0.050)
Sierra Leone						
"Sierra Leone" (I)	BMNH	14° W, 8° N	North Equatorial	1.34 (NA)	0.76 (NA)	1.76 (NA)
"Sierra Leone" (II)	BMNH			1.35 (0.059)	0.73 (0.067)	1.72 (0.067)
Freetown (I)	BMNH			1.41 (NA)	0.77 (NA)	1.72 (NA)
"Sierra Leone" (III)	BMNH			1.35 (NA)	0.73 (NA)	1.67 (NA)
Freetown (II)	BMNH			1.36 (0.052)	0.73 (0.096)	1.72 (0.070)
"Sierra Leone" (III)	BMNH			1.32 (0.056)	0.73 (0.029)	1.67 (0.070)
Freetown (III)	BMNH			1.35 (0.065)	0.73 (0.045)	1.73 (0.063)
Virgin Islands	ANSP	65° W, 17° N	Caribbean	1.53 (0.105)	0.76 (0.065)	1.94 (0.238)

TABLE 2. Shell sculpture characteristics identified or measured.

Character	Measurement type
# whorls in the protoconch	numeric
# whorls in the telochonch	numeric
whorl # in which primary grooves first occur	numeric
# primary grooves at first appearance	numeric
whorl in which axial striae occur	numeric
whorl in which secondary grooves first occur	numeric
regularity of secondary grooves	categorical (0: irregular; 1: regular)
presence/absence of tertiary grooves	categorical (0: absent; 1: present)
whorl in which tertiary grooves first occur	numeric
presence/absence of spiral striae	categorical (0: absent; 1: present)
whorl in which spiral striae first occur	numeric
columella shape	categorical (0: concave; 1: vertical; 2: convex)
columella pinching	categorical (0: pinched; 1: unpinched)
columella color	categorical (0: creamy yellow; 1: otherwise)

base and lip (Fig. 2, Table 2). Shell color is variable, and two distinct color morphs, normal and orange, have been identified. The ground color of the "normal" color morph is creamy yellow to reddish-brown, and is overlaid with flecks of dark orange and brown. The ground color of the "orange" morph is light orange or yellow, and it is overlaid with faint orange flecks. Normal morphs were assigned a value of zero, and orange morphs, one.

Genital characteristics were measured for dissected specimens only (Figs. 4, 5). Length of the penis and pallial oviduct, diameter of the spiral portion of the oviduct, and length of the bursa copulatrix were measured with an ocular micrometer.

Statistical Analysis

We used discriminant analysis, cluster analysis, and principle components analysis (PCA), in SYSTAT version 7.0 (SPSS, 1997) and S-Plus for Windows version 4.0 (MathSoft, 1997), to compare morphological variation within and among populations. Because many of the samples were from sites close to each other (e.g., from within the same country), we grouped the sites into 19 discrete geographic "locations" for most of the analyses. Location groupings are indicated in Table 1. Data were transformed when necessary to meet assumptions (approximate normality, homoscedasticity) of all statistical tests (see Kroonenberg et al., 1997, for transformations appropriate for categorical data prior to application of these multivariate analyses). Details of each technique are given along with their associated results in the following section.

RESULTS

Geographic Patterns in Shell Shape

Shell shape showed pronounced changes from east to west among samples. Shells from the Western Atlantic and Caribbean have comparatively high spires and more circular apertures (Table 1, Fig. 6). The thickness of the columella also increases from east to west. Shells from the Eastern Atlantic have more whorls per mm of shell height. Primary grooves appeared earlier and in larger numbers, whereas secondary grooves occurred later on shells from the Eastern Atlantic. Discriminant analysis using these eight morphological variables (proportionality, circularity, and spire height, columellar thickness, whorls/mm, number of primary grooves, whorl on which primary and secondary grooves first appear, all expressed in standard deviation units) correctly identified 85% of the shells as coming from either the Eastern or Western Atlantic ($F = 106.6$, $P < 0.0001$; Table 3). However, shells from four localities generally were misclassified at this coarse level of geographic resolution. Shells from Liberia and Senegal were routinely assigned to the Western Atlantic, shells from Brazil were assigned more commonly to the Eastern Atlantic (Table 3), and shells from Gabon were assigned equally to each side of the Atlantic. Spire height, whorls/mm, columellar thickness, and number of primary grooves were the principle variables that discriminated between shells of the Eastern and Western Atlantic.

To investigate the hypothesis that morphological variation was associated with potential dispersal routes, we classified sites according

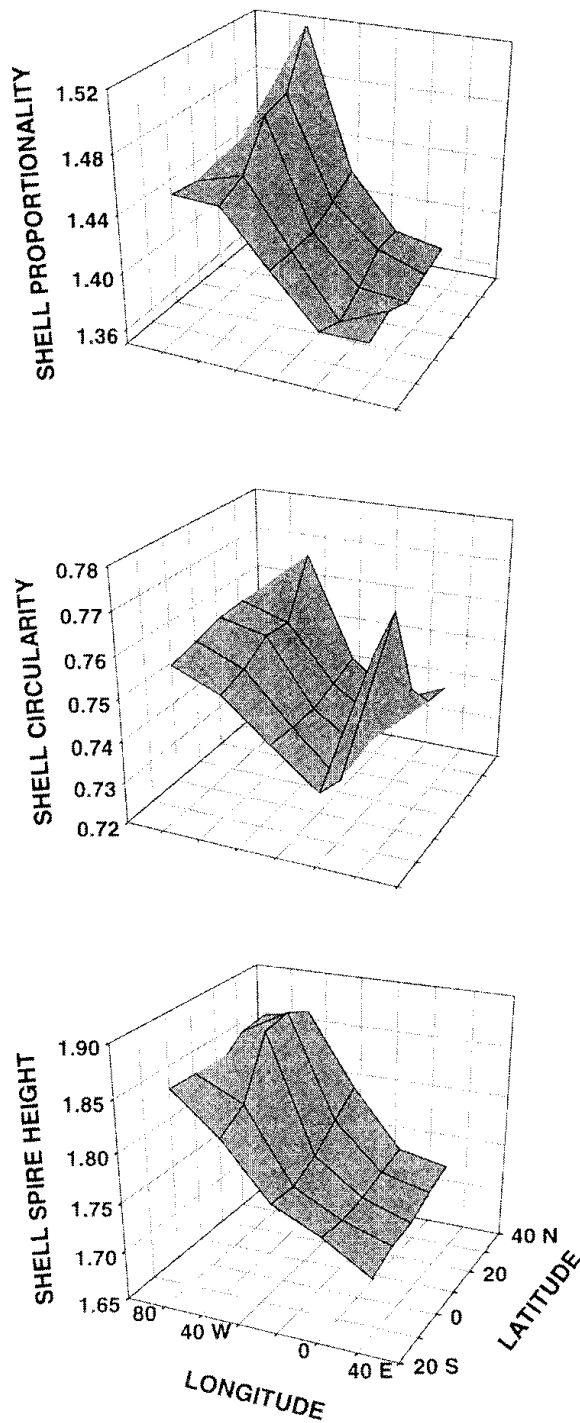


FIG. 6. Clinal patterns in shell proportionality, circularity, and spire height. Illustrations are distance-weighted, least-squares smoothing through data from all 41 sites.

to the predominant current affecting them (Caribbean, Gulf of Mexico, Gulf Stream, North Equatorial, South Equatorial; see Fig. 1; *a priori* current classifications in Table 1). We then used discriminant analysis to see if shells could be classified correctly with re-

TABLE 3. Percent of shells correctly identified by discriminant analysis as coming from either the Eastern or Western Atlantic. Bold type indicates overall discrimination. Normal type indicates discrimination among locations within either the Eastern or Western Atlantic.

Location	%
Eastern Atlantic	84
Angola	84
Congo	70
Gabon	50
Ghana	95
Liberia	33
Nigeria	91
Principe Islands	100
Senegal	10
Sierra Leone	96
Western Atlantic	85
Bahamas	76
Belize	83
Bermuda	91
Brazil	40
Cuba	68
Florida	90
Haiti	88
Jamaica	84
Nicaragua	75
Virgin Islands	95

spect to these prevailing currents. Using the same eight standardized morphological variables, we could classify correctly 61% of the shells overall with respect to current of origin ($F = 51.7$, $P < 0.0001$). The most important morphological variables contributing to discrimination according to prevailing current were whorls/mm, spire height, columellar width, and shell circularity. In total, we could correctly classify 75% of shells from sites associated with the North Equatorial current, 71% from the South Equatorial current, 66% from the Gulf Stream, 64% from the Gulf of Mexico, and 40% from the Caribbean.

Within each current grouping, most shells from most locations were correctly classified into their respective current regimes (Fig. 7). Exceptions included Nicaragua (generally assigned to the South Equatorial current instead of the Caribbean); Brazil and Liberia (all assigned to the South Equatorial current instead of the North Equatorial current); Senegal (assigned to either the Caribbean or South Equatorial current instead of the North Equatorial current); and Gabon (30% of which were assigned to the Caribbean current). Shells from the Caribbean islands of Cuba and Jamaica frequently were assigned to the Gulf of Mexico or the Gulf Stream, whereas shells from

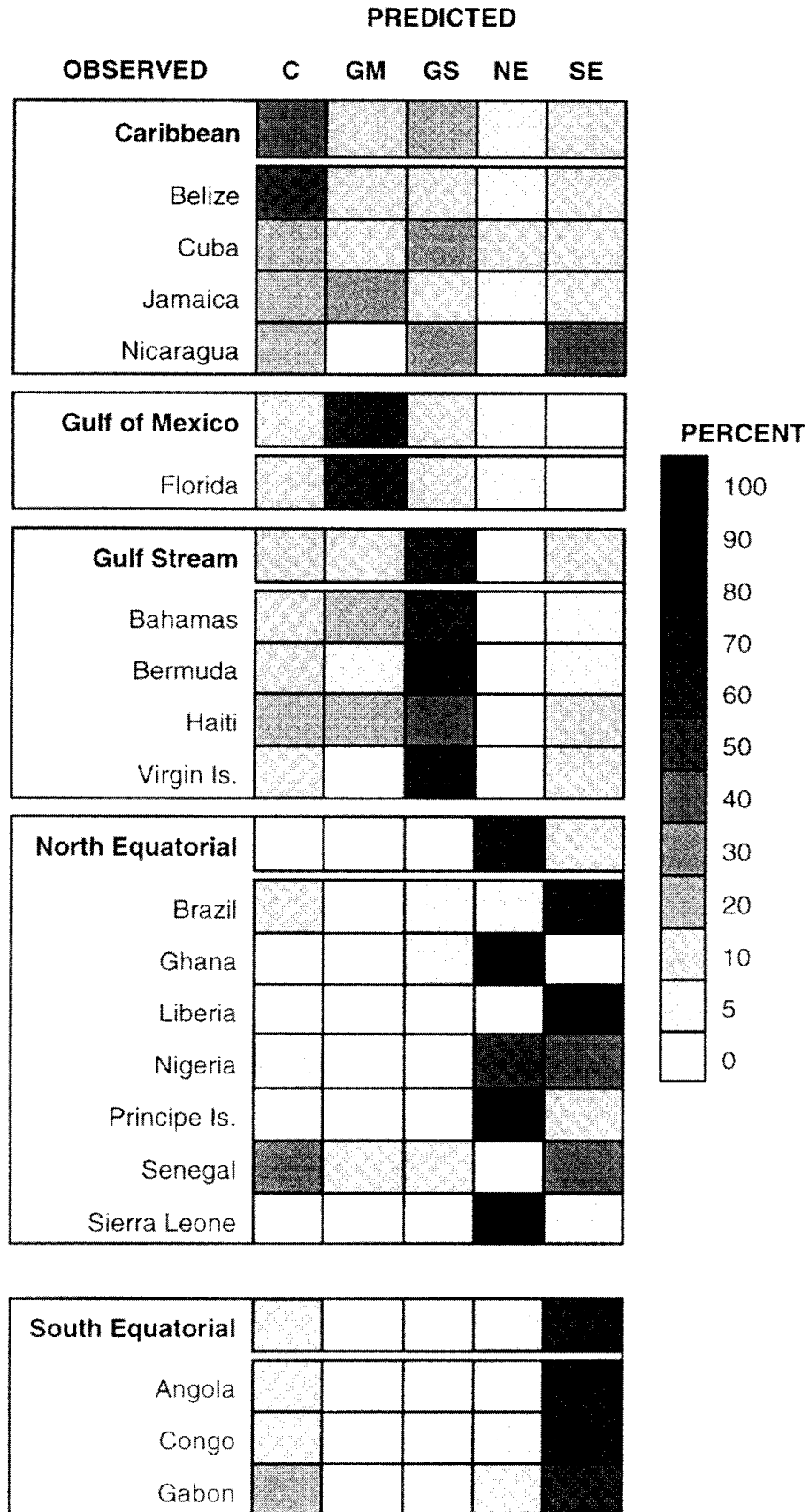


FIG. 7. Classification matrix resulting from discriminant analysis of shells from the five prevailing currents. Shading indicates percent classification into each of the five currents, with shading increasing with percentage. For each current, the overall classification is given in the first row (label in bold type), followed by the classification for each locality within that current grouping. Predicted current groupings: C—Caribbean; GM—Gulf of Mexico; GS—Gulf Stream; NE—North Equatorial; SE—South Equatorial.

TABLE 4. Loadings of shell morphological variables on the first four principal component axes. Only loadings $\geq |0.1|$ are shown. The first four axes account for 90% of the among-location variance in shell morphology. Characters are ordered in descending order of their loadings on the first principal axis.

Variable	Axis 1	Axis 2	Axis 3	Axis 4
Thickness of columella	0.476	-0.170	-0.186	-0.318
Shell proportionality	0.471		0.401	
Whorls/mm of shell height	-0.464	0.180		0.348
Shell spire height	0.385		0.582	0.249
Whorl on which secondary groove first appears	0.276	0.503	-0.345	0.256
Number of primary grooves	0.234	-0.433	-0.457	
Whorl on which primary groove first appears	0.197	0.603	-0.326	
Shell circularity	0.137	-0.353	-0.159	0.803
Cumulative proportion of variance explained	0.42	0.66	0.78	0.90

Haiti (collected on the northern [Gulf Stream] side of the island) were mis-assigned to either the Caribbean or Gulf of Mexico.

Our eight shell morphology characteristics explained 90% of the among-location variance identified by principal components analysis (Table 4). Columellar width, proportionality, whorls/mm, and spire height loaded most heavily on the first axis, whereas whorl on which primary and secondary grooves first appeared, number of primary grooves, and shell circularity loaded most heavily on the second axis (Table 4, Fig. 8). Shells from Principe, Ghana, Sierra Leone, Nigeria, and Angola were distinguished from the others because of their low spire height and shell proportionality and their relatively large numbers of whorls/mm of shell height (Fig. 8). In other words, these five locations had the most globose shells. Shells from Angola, Congo, and Gabon had the most circular apertures (Fig. 8). Shells from the Virgin Islands, Nicaragua, Senegal, and Cuba were relatively high spired, and shells from the Virgin Islands and Bermuda had the thickest columellae.

Cluster analysis similarly illustrated the groupings of sampling localities according to these eight morphological variables (dendrogram not illustrated). We identified five clear groupings of locations from the complete-linkage dendrogram resulting from our cluster analysis: (1) Principe, Ghana, and Sierra Leone; (2) Congo, Gabon, Angola, Nigeria, and Brazil; (3) Liberia, Senegal, and Nicaragua; (4) Belize, Haiti, Jamaica, the Bahamas, Cuba, and Florida; (5) Bermuda and the Virgin Islands.

Habitat-Specific Patterns in Shell Shape

Climatic properties, stature of the mangrove forests of each location (Table 5), and primary

nutrient source (oligotrophic vs. estuarine) were used to test for relationships between habitat characteristics and shell morphology. As with the morphology data, we first ordinated the sites according to the five variables using PCA. The loadings of the variables for the first two principal axes are shown in Table 6. The first axis is a function primarily of average canopy height and nutrient source (estuarine vs. oligotrophic), whereas the second axis is a function primarily of annual temperature and amount and pattern of rainfall. Together, these two composite axes encompassed 70% of the among-habitat variance. Standardized morphological and habitat scores for each location were computed by multiplying each variable by the factor coefficient derived from the PCAs morphological and habitat data, respectively. These products were then summed to yield a single standardized morphological or habitat score (computations done in Systat version 7.0). For clarity, we only illustrate the standardized scores based on the factor coefficients of the first principal component axis from each analysis. The result of this computation is a single composite morphological score and a single composite habitat score for each of the 19 locations. We found a significant association between these two scores ($r = 0.54$, $P = 0.018$; Fig. 9), which indicated a significant correlation of overall shell morphology with their local environment. This figure also illustrates clearly the similarity in overall shell morphology and habitat of Brazil, Nicaragua, and all the African samples.

Shell Color

Most shells had "normal" coloration; of the total sample, 68 shells (6.5%) were the "orange" morph. No differences in relative fre-

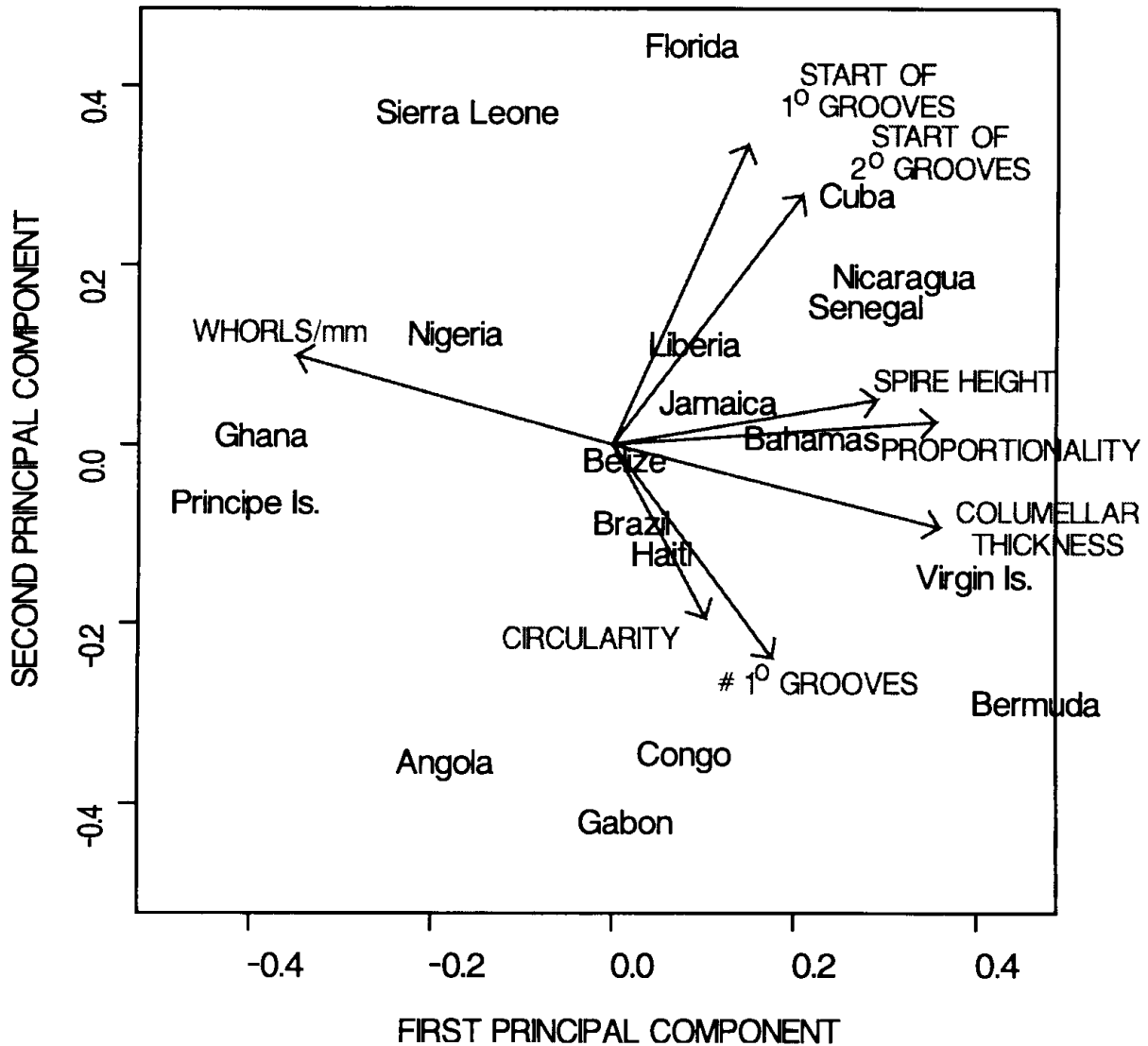


FIG. 8. Principal components biplot illustrating placement in ordination space of the 19 sampling locations with respect to eight morphological variables. All variables were standardized prior to analysis. Loadings for these two component axes, as well as axes three and four, are given in Table 4.

quencies were found between shells from the eastern and western Atlantic ($\chi^2 = 0.823$, $P = 0.360$, Fisher's Exact Test). Among current regimes, both the Gulf Stream and South Equatorial samples had more orange morphs than expected by chance alone (13.9% and 24%, respectively, $\chi^2 = 36.096$, $P < 0.001$, G-test). This result was due to unusually high frequencies of the orange morph in samples from Angola (24%), Bermuda (36.4%), and Virgin Islands (20%). Shell color was not clearly associated with any habitat-specific variable.

Genitalia

The pallial oviduct of the ovoviviparous *L. angulifera* has a single spiral loop that passes

through the albumen and membrane glands (Fig. 4), unlike the pallial oviduct of oviparous congeners, which have four to six loops that contain additional capsule glands through which the eggs must pass before being released. The penial glandular disc is round, flattened, and darker in color than the rest of the penis, and the open sperm groove runs along the filament (Fig. 5). All specimens from which the penis was removed and drawn showed a remarkable uniformity in shape and size (Table 7). Additional multivariate analysis of sites for which we measured genital characteristics showed that those populations were distinguishable based only on characteristics of the pallial oviduct, which was much longer at one Florida site and at Wee Wee Cay than at the other sites. However, absolute

TABLE 5. Habitat characteristics of the 19 locations. Data from Walter et al. (1975); Wilcox et al. (1975); Ward & Bunyard (1992); Suman (1994); Saenger & Bellan (1995); Spalding et al. (1997).

Location	Annual rainfall (mm)	Number of dry months	Mean monthly temp. (°C)	Mean canopy height (m)	Nutrient source
Eastern Atlantic					
Angola	363	9	26.4	30	estuarine
Congo	1306	4	25.3	30	estuarine
Gabon	1904	4	26.3	30	estuarine
Ghana	858	6	26.5	15	estuarine
Liberia	3874	3	27.0	30	estuarine
Nigeria	1830	4	26.3	12	estuarine
Principe Islands	721	4	26.2	5	oligotrophic
Senegal	516	8	24.0	4	estuarine
Sierra Leone	4349	4	26.6	35	estuarine
Western Atlantic					
Bahamas	1181	2	25.1	3	oligotrophic
Belize	1500	2	29.5	8	oligotrophic
Bermuda	1483	0	21.4	3	oligotrophic
Brazil	2150	4	26.4	30	estuarine
Cuba	1481	3	25.2	10	oligotrophic
Florida	1004	1	25.3	10	oligotrophic
Haiti	1242	6	27.5	10	oligotrophic
Jamaica	800	3	26.4	12	oligotrophic
Nicaragua	3293	0	26.0	15	estuarine
Virgin Islands	1638	0	26.4	5	oligotrophic

TABLE 6. Loadings of habitat variables on the first two principal component axes. Only loadings $\geq |0.1|$ are shown. These two axes account for 70% of the among-location variance in habitat. Characters are ordered in descending order of their loadings on the first principal axis.

Variable	Axis 1	Axis 2
Canopy height	0.898	0.122
Nutrient source	0.832	-0.207
Annual rainfall	0.525	0.788
Number of dry months	0.504	-0.807
Average annual temperature	0.412	0.133
Cumulative proportion of variance explained	0.44	0.70

shell height and pallial oviduct length were significantly correlated ($r^2 = 0.54$; $P = 0.024$), so this result simply shows that large snails had large pallial oviducts. On the other hand, shell height and penis length were not correlated ($r^2 = 0.17$; $P = 0.27$) among these sites.

DISCUSSION

Our data illustrate substantial variation in shell morphology in *Littoraria angulifera*, and this variation is associated both with potential dispersal paths and local habitat conditions. Despite an 8–10 wk planktonic larval stage, long enough to cross the Atlantic on any of the

trans-Atlantic currents, populations associated with different current regimes exhibit clear and strong differences in shell morphology (Figs. 6, 7, Table 3). This observation on first glance supports the hypothesis that regional diversification associated with dispersal is occurring in this species. The strong association of habitat types with geography (Table 5), however, lends some credence to the hypothesis that morphological variation is determined primarily by local environmental conditions. Furthermore, the principal exceptions to the dispersal-morphology association (Fig. 8), namely shells from Senegal, Liberia, Brazil and especially Nicaragua (which is well-isolated from easy trans-Atlantic dispersal via either equatorial current), and the uniformity in genital form and size from snails from both sides of the Atlantic (Table 7) suggest that we should reject the hypothesis of regional diversification associated with dispersal as a cause for morphological variation in *L. angulifera*.

Littoraria angulifera inhabits mangrove swamps, and we hypothesize that observed variation in its shell morphology is most likely caused by habitat-specific differences in nutrient status associated with local climate, forest structure, and prevailing geomorphology. Mangrove swamps in Florida, the Bahamas, and the Caribbean Islands are primarily found on carbonate platforms and are markedly oligotrophic (nutrient-poor) relative to the more

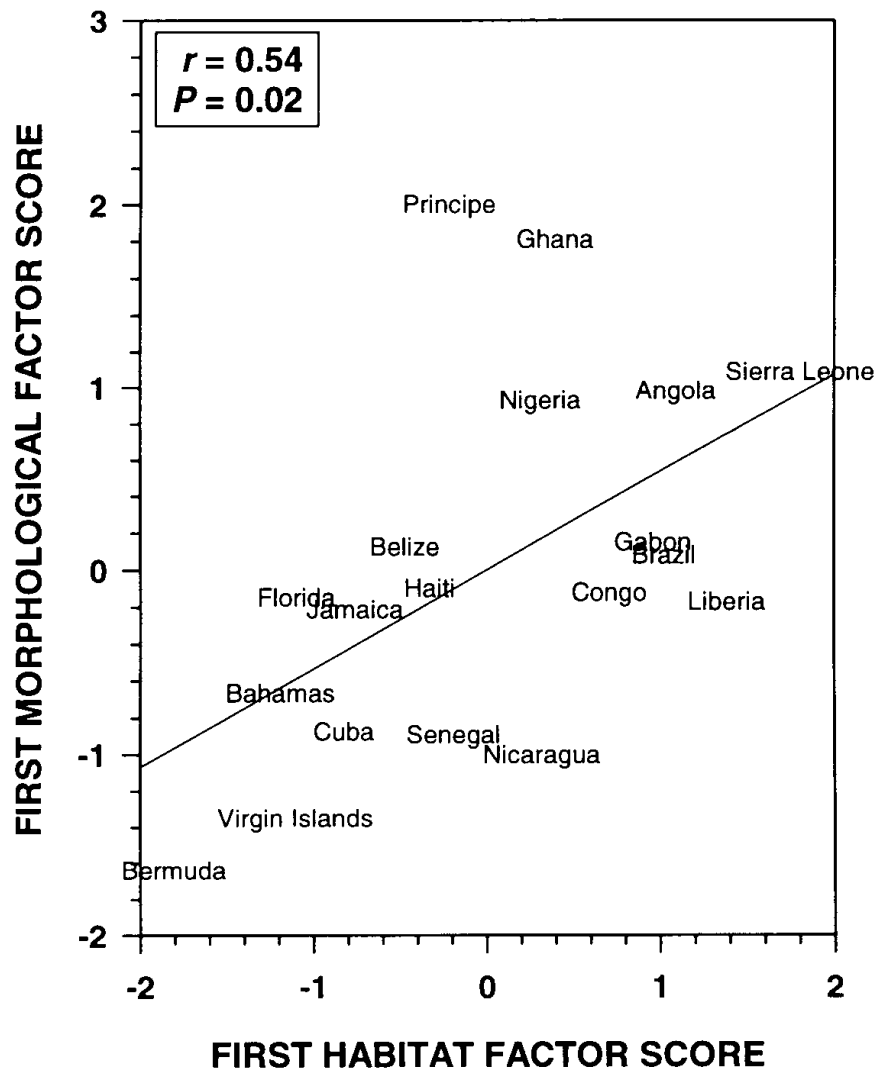


FIG. 9. Association between standardized habitat and shell morphology scores for the 19 locations.

TABLE 7. Measurements of genital characteristics (means in mm with standard deviations in parentheses). All values are lengths, except for diameter of the spiral portion of the pallial oviduct. Sample size for neotropical samples = 20; for African samples = 6.

Sample site	Penis	Pallial oviduct	Spiral Portion	Bursa copulatrix
Florida: Cockroach Bay	2.5 (2.5)	1.9 (2.2)	0.7 (0.9)	1.2 (1.5)
Florida: Little Shark River (mouth)	2.7 (3.0)	2.6 (2.8)	0.9 (1.0)	1.8 (2.1)
Florida: Little Shark River (middle)	3.1 (3.9)	4.1 (4.2)	1.7 (1.9)	2.8 (3.0)
Florida: Little Shark River (upper)	2.0 (2.9)	2.6 (2.5)	0.9 (0.9)	1.9 (1.9)
Florida: Hurricane Island	2.3 (2.8)	2.1 (2.0)	0.9 (0.9)	1.3 (1.2)
Belize: Wee Wee Cay	2.4 (3.6)	3.5 (2.6)	1.7 (1.2)	2.1 (1.6)
Jamaica: St. Anne's Bay	2.7 (2.7)	1.7 (2.1)	0.7 (0.8)	1.1 (1.4)
Ghana	1.9 (2.4)	1.0 (1.1)	0.3 (0.4)	0.8 (0.9)
Sierra Leone: Freetown (II)	2.5 (3.4)	1.7 (2.6)	0.5 (0.4)	1.9 (2.1)

eutrophic (nutrient-rich) estuarine mangroves of Africa, Nicaragua and South America (e.g., Twilley, 1995). Oligotrophic swamps have higher salinity and water clarity (Twilley, 1995), and may be associated with lower fungal bio-

mass on the leaves where *L. angulifera* feeds (Kohlmeyer & Bebout, 1986) than estuarine ones. Lower food availability and higher salinity may result in slower growth rates of *L. angulifera*. Kemp & Bertness (1984) demon-

strated experimentally that well-fed, fast-growing *Littorina littorea* produce more rounded, globose shells (like *L. angulifera* from most of Africa, Nicaragua, and Brazil), while poorly fed, slower-growing *Littorina littorea* produced more pointed, high-spired shells (like *L. angulifera* from Florida and the Caribbean). Boulding & Hay (1993) found, in contrast, that well-fed *Littorina subrotundata* produces high-spired shells. Additional experimental work is needed to assess the role of food availability on shell shape in *L. angulifera*, and in littorines in general.

The high-spired shells from Senegal occur in short-statured mangrove forests that are more like those of the Caribbean than the rest of the sampled African locations (Table 5, Fig. 10). Caribbean and Senegalese mangroves are short (generally < 10 m) with relatively open canopies, and in such forests, insolation is likely to be higher and evaporation greater. It is likely that snails in these forests experience higher mid-day temperatures than snails in mangroves with tall, closed canopies. This observation, along with the strong association of canopy height with the first principal axis of the habitat PCA and rainfall and average temperature on the second principal axis of the habitat PCA strongly suggests that shell shape in *L. angulifera* is associated with desiccation resistance (Fig. 9 links the morphology and habitat PCAs.)

Shell sculpturing may also be associated with food availability (Berry, 1961; Janson, 1982a) and desiccation resistance (Vermeij, 1973). Vermeij (1973) suggested that even very small variations in shell sculpture may reduce desiccation as grooves may serve to reflect heat and cause cooling through convection. Shell sculpture characteristics (number and location of primary and secondary grooves) loaded heavily on the first two principal components axes (Table 4) in the analysis of shell morphology. Figure 9 suggests additional linkages between shell sculpture and habitat characteristics. For example, shells from Bermuda, the Virgin Islands, Congo, Gabon, and Senegal are distinguished from the others by relatively many primary grooves, and mangrove forests in these areas are sparse and short in stature, or occur in regions with pronounced dry seasons (Chapman, 1976). Note that despite exceptionally low rainfall and a 9-month dry season, the canopy height in Angolan mangrove forests is very high as a consequence of high nutrient input in Angolan estuaries. We infer that the lower sur-

face temperatures, reduced rate of evaporation, and increased nutrient levels leads to snails with globose shells (Table 1). Shell color polymorphism in *Littoraria* may also be associated with desiccation avoidance (Cook, 1983; Cook & Freeman, 1986; but see Reid, 1987), but we lack detailed microclimatic data for any of these sites. In a preliminary study, however, we found no association between substrate temperature, insolation, and frequency of orange morphs of *L. angulifera* at Wee Wee Cay, Belize (A. M. Ellison, unpublished data). We note also that the frequency of rare, orange morphs of *L. angulifera* is likely to be artificially high in museum samples because of collecting bias.

Observed variation in columellar thickness may be associated with predation, but we know little about predators of *L. angulifera* and other supralittoral littorinids. Reid (1985, 1986, 1988, 1992) suggests that grapsid crabs prey on *Littoraria* in Pacific mangrove forests, and omnivorous grapsids do occur in Atlantic mangroves (Sterrer, 1986). However, there have been no studies of their diets. Shell color polymorphism may also be associated with predation (Reimchen, 1979; Cook, 1983; Reid, 1988; Cook & Kenyon 1993). Further study of both microclimate and predators of *L. angulifera* is needed, especially in Bermuda, the Virgin Islands, and Angola, where we recorded exceptionally high frequencies of orange shell morphs.

We observed site-specific differences in pallial oviduct length that were correlated with shell size, but penis length was invariant with respect to shell size. This result is not unexpected because a larger pallial oviduct would be associated with increased clutch size in larger snails. Comparable variability in penis length, however, could limit male reproductive success.

Genetic variability underlies morphological variation in some littorinids (Janson, 1982b; Cook, 1992; Cook & Garbett, 1992; Mill & Grahame, 1995). Although the lengthy larval stage (Gallagher & Reid, 1979) and likelihood of regular gene-flow among populations (at least those within current regimes) suggests that genetic differentiation among local populations of *L. angulifera* is unlikely, Janson (1985) found unexpectedly high genetic variation among Florida populations of *L. angulifera*. Janson (1985) attributed this variation either to differential selection due to abiotic factors and predation, or to restricted gene flow due to limited larval dispersal affected by

current distribution. Larger genetic divergence was found between Gulf Coast and Atlantic Coast populations of *L. angulifera* than was found among populations on either side of the peninsula. In another study of genetic variability in *L. angulifera* within the Gulf of Mexico however, Gaines et al. (1974) found no differences between observed and expected numbers of heterozygous individuals in 19 of 20 island populations.

Linking larval dispersal, distribution, and variability of genetic and phenotypic origin in oviparous and ovoviviparous gastropods is complicated by the lack of knowledge concerning the pelagic portion of the larval stage; laboratory breeding experiments and rearing of larvae generally have been unsuccessful (McQuaid, 1996). Nonetheless, more systematic study of local and regional morphology, and further genetic study of these populations, combined with the results of this study based on opportunistic museum collections would provide a more complete explanation of observed geographic and habitat-specific morphological variation of *Littoraria angulifera*.

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