Diversity Trends in Coral-Inhabiting Barnacles (Cirripedia, Pyrgomatinae)[1]

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Introduction

A recent revision of the coral-inhabiting barnacles of the subfamily Pygromatinae (Ross and Newman, 1973) covers various aspects of the biogeography, growth and form, and host specificity, as well as systematics and evolution, and thereby affords an up-to-date source for analyses of diversity trends in the group.

A variety of barnacles inhabit the skeletons of living corals and/or limestones usually associated with them. Members of the order Acrothoracica, and *Lithotrya* among the lepadomorphans, excavate their way into calcareous substrates and are therefore "burrowing barnacles" (Darwin, 1854; Tomlinson, 1969). However, these barnacles have not become specifically modified in form or in their manner of growth for intracoralline life and more often than not occur in stable or eroding substrates. On the other hand, a number of balanid species are obligate coral symbionts, and those that have become markedly specialized in growth and form for this relationship constitute the Pyrgomatinae (Baluk and Radwański, 1967; Ross and Newman, 1973—complete bibliography). The subfamily is distinguished from other members of the Balanidae that inhabit corals in having a wall of four plates (or totally concrescent) rather than the usual six, and by a growth pattern that allows them to keep pace with the advancing surface of the coral for a considerable period of time (several years) before becoming entombed.

Several workers consider the Pyrgomatinae to be polyphyletic (Withers, 1929; Utinomi, 1967). Ross and Newman (1973) define three lineages (Tropical Atlantic, Indo-Pacific and Cosmopolitan), and Newman and Ladd (1974a) demonstrate the existence of an intermediary Miocene form (*Eoceratoconcha*) that, if extant, would preclude the formal separation of the Caribbean pyrgomatine *Ceratoconcha* from the Balaninae. On the other hand Newman and Ladd (1974b) report the occur-

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[1] Contribution of Scripps Institution of Oceanography; supported in part by a grant (GB-30908X) from the National Science Foundation. Paper presented at a Symposium on "Animal associates on coral reefs", International Symposium on Indo-Pacific Tropical Reef Biology, Guam and Palau, June 23–July 5, 1974.

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Micronesica 12(1): 69–82. 1976 (June).

rence of rather specialized "modern" forms (*Savignium* and *Nobia*) from Miocene deposits in the western Pacific.

The tropical Atlantic Pyrgomatinae, consisting of the rather generalized genus *Ceratoconcha* of perhaps three extant species presently limited to hermatypic scleractinians in the Caribbean and Gulf of Mexico, was more speciose in the Miocene than it is today (Baluk and Radwański, 1967; Newman and Ladd, 1974a). While this seems likely also for the Indo-Pacific group, as apparently it was for the insular Mollusca (Ladd, 1960), an adequate fossil record is lacking. Presently represented by eight genera containing 35 species, the Indo-Pacific group is relatively diverse and its members range, in two major phylogenetic branches, from quite generalized to highly specialized forms. The cosmopolitan group on the other hand includes several species in the relatively generalized genus *Boscia*. One occurs in ahermatypic deep-water corals in the eastern Atlantic (Rees, 1962), the second and third in hermatypic scleractinians in the Caribbean and southern Japan.

Whether or not these three groups are considered to be polyphyletic, analyses of diversity trends must take their ecological and geographical separations into consideration. Likewise, for a given faunal province, completeness of the data available and biological considerations must be kept in mind. Therefore, the following analysis will deal with the Pyrgomatinae as a whole, or with certain groups. The diversity trends to be considered will be derived from correlations among four principal indices related to 1) Structural Diversity, 2) Generic Species Richness, 3) Host Exploitation and 4) Geographical Distribution. Finally, the relationship between current geographic range of the barnacle genera and the average generic age of the host coral genera will be explored.

Structural Diversity

Ross and Newman (1973) present a figure illustrating the phylogenetic relations within the Pyrgomatinae, reproduced here for easy reference (Fig. 1, A). It will be observed that *Cantellius*, the most generalized of the Indo-Pacific group, resides at the base of the diagram where it is flanked by the more or less equally generalized Atlantic Group (*Ceratoconcha*) and the Cosmopolitan group (*Boscia*). *Cantellius*, in being sufficiently generalized, represents a model from which the two major Indo-Pacific phylogenetic lines can be derived. The structurally most specialized forms, *Creusia, Nobia, Pyrgoma, Pyrgopsella* and *Hoekia,* are deployed across the top of the diagram, in accordance with their inferred phylogenetic connection through *Hiroa* and *Savignium.* It should also be noted that not only do these forms stand at the top of their respective lines, but their positions are "ranked" horizontally, by degree of skeletal complexity, from left to right.

The questions we would now like to explore depend in good part upon quantifying the degree of specialization seen in each step in the phylogenetic series presented in Figure 1, A. To quantify the illustrative data, the walls and valves can be arranged serially, according to their departure from the stem form, and then numbered con-

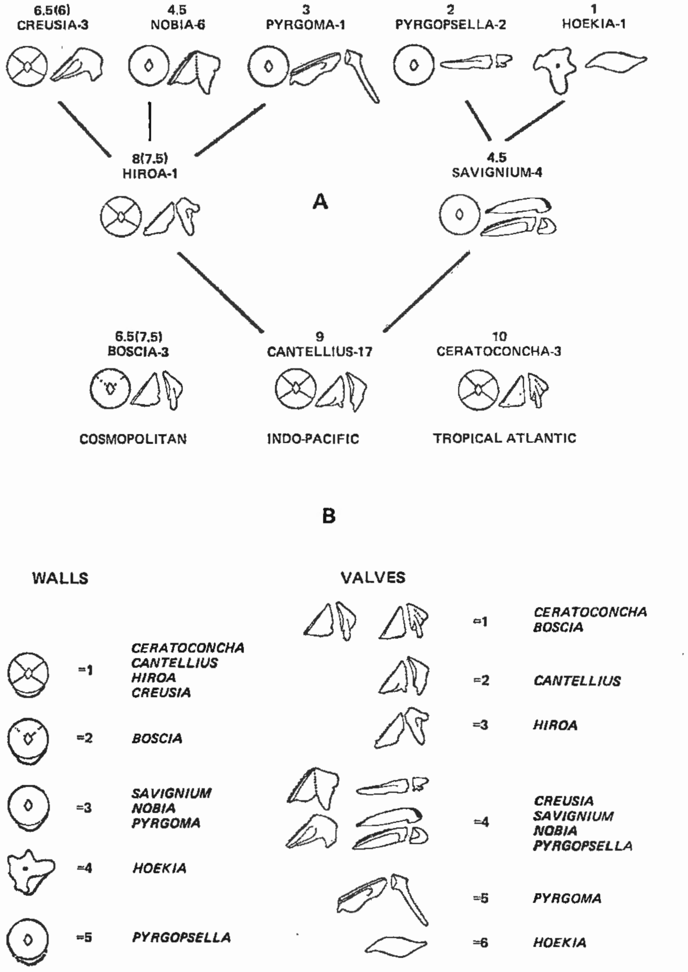

Fig. 1. A, Phylogenetic relationships within the Pyrgomatinae (after Ross and Newman, 1973). Numerals following generic names indicate the number of species representing each. Numerals above are the structural diversity indices found in Table 1 herein; those in parentheses are the changes in rank-order introduced when the indices are formed by addition rather than multiplication. B, wall and valve types, in order of increasing specialization, the genera they represent and the arbitrary values assigned to them.

secutively (Fig. 1, B). The values thus obtained appear in two adjacent columns following the generic names to which each applies (Table 1, A: W & V). The W-column is arranged in order. In the V-column, the values fall where they must. A visual comparison suggests a similar but imperfect trend. The question now is, how good is the trend? The data can readily be subjected to a rank-difference correlation analysis (Tate and Clelland, 1957). The rank-difference coefficient; $r_d=1-\{6\sum d^2/N(N^2-N)\}$ (where d=difference between ranks of paired values and

Table 1. A, correlation of structural modifications between walls (W) and valves (V) derived from values assigned in Figure 1, B; B, structural diversity indices (SDI) formed by multiplication or addition, and corresponding rank-values.

A	W	r	V	r	B	W	V	SDI		ranks	
Ceratoconcha	1	2.5	1	1.0	*Ceratoconcha*	1	1	1	(2)	10	(10)
Cantellius	1	2.5	2	2.5	*Cantellius*	1	2	2	(3)	9	(9)
Hiroa	1	2.5	3	4.0	*Hiroa*	1	3	3	(4)	8	(7.5)
Creusia	1	2.5	4	6.5	*Creusia*	1	4	4	(5)	6.5	(6)
Boscia	2	5.0	2	2.5	*Boscia*	2	2	4	(4)	6.5	(7.5)
Savignium	3	7.0	4	6.5	*Savignium*	3	4	12	(7)	4.5	(4.5)
Nobia	3	7.0	4	6.5	*Nobia*	3	4	12	(7)	4.5	(4.5)
Pyrgoma	3	7.0	5	9.0	*Pyrgoma*	3	5	15	(8)	3	(3)
Hoekia	4	9.0	6	10.0	*Pyrgopsella*	5	4	20	(9)	2	(2)
Pyrgopsella	5	10.0	4	6.5	*Hoekia*	4	6	24	(10)	1	(1)
	$r_d=0.731$ $(p<.02)$										

N=number of items ranked) can range from $+1$ through zero to -1; that is, from a perfect direct to a perfect inverse correlation. The square of the coefficient approximates the percent variability of one factor explained by the other variable, and confidence limits can be obtained from an appropriate table (Tate and Clelland, 1957).

The r_d between ranks W and V (Table 1, A) of 0.73 (53%; $p<0.02$), indicates a significant correlation between the degree of modification of the wall and that of the valves. This justifies combining values to form Structural Diversity Indices (SDI).

W and V values can be either added or multiplied in forming the indices, and either way the rank order comes out much the same (Table 1, B). The tie between *Creusia* and *Boscia* in the first ranking shifts to *Boscia* and *Hiroa* in the second, but this does not adversely affect phylogenetic considerations (see below). Since both *Boscia* and *Hiroa* will be excluded for various reasons in subsequent calculations, other possible implications of this shift will be ignored. In order to avoid inverse correlations, the SDI ranking has been reversed so that the most generalized genera have the largest indices.

SDI rank-order values can now be used to quantify the phylogenetic scheme proposed by Ross and Newman (1973). It will be observed in Figure 1, A that where W and V are multiplied, the ties, between *Nobia* and *Savignium*, and *Creusia* and *Boscia*, are of no obvious consequence since the genera involved reside in different lineages. It seems appropriate then to go ahead and use the SDI values obtained by multiplication in comparisons with other biological and physical parameters.

Structural Diversity and Host Exploitation

Ross and Newman (1973: 145, Fig. 4) graphically portray the distribution of pyrgomatine genera, except for *Pyrgopsella* which occurs on sponges, among the scleractinian coral suborders and the hydrocoral *Millepora.* The diagram also indicates the relative number of coral genera in each suborder known to support members of each barnacle genus, and the relative frequencies with which the barnacle genera have been reported in the literature to occur on genera of each suborder. This diagram indicates that the faviine corals are exploited by a greater variety of relatively frequently reported barnacles than are the other corals, that the most prominent barnacle genus (*Savignium*) on faviines is the only one to infect milleporines, that all but two genera are distributed between two or more coral suborders, and soforth. By comparing these facts with the phylogenetic diagram (Fig. 1 A, herein), it will be noted that faviine-dominant *Savignium* not only contains a species that has adapted to living on a hydrocoral, but it is also the model from which the sponge inhabiting *Pyrgopsella* and the wholly parasitic *Hoekia* must have been derived. Interestingly, *Savignium* ranks 4.5 on the SDI scale (Table 1, B)—that is, it is in the moderately specialized sector of the scale. Similar comparisons also reveal that the morphologically most specialized genera *Hoekia, Pyrgopsella* and *Pyrgoma,* having SDI rank-values of 1, 2, & 3 respectively, have not diversified within the groups in which they occur. It would appear then that the moderately specialized, or even the generalized genera, occupy a greater variety of hosts than do the extreme specialists. Since we have quantified structural diversity (SDI), we need only form Host Exploitation Indices (HEI) and a rank-difference analysis can readily be carried out.

To obtain Host Exploitation Indices (HEI), the number of host genera for each barnacle genus was multiplied by the number of suborders or other higher categories they represented. Forming the index in this way favors genera occupying a number of higher categories over genera occupying the same number of host genera within fewer higher categories. If we were dealing with species rather than genera, there would probably be no objection to this approach in that species, not genera, perpetuate themselves. Since we are not concerned with perpetuation here, but rather with a measure of the degree to which life-forms have diversified, treating genera in this way also seems conceptually sound.

The HEI values can now be compared to the SDI values. The coefficient calculated (Table 2, A, r_d=0.485), while indicating a trend, is not particularly compelling evidence for a relationship between being structurally generalized and occupying a wide variety of hosts.

An inspection of the HEI column (World-wide), reveals that *Hiroa,* having an SDI of 8 and an HEI of 2, causes a large part of the difficulty. *Hiroa* is a new genus known from specimens discovered in a single piece of coral removed by high explosives from the surf zone of the reef front in the Central Caroline Islands (Ross and Newman, 1973). This habitat, the "Mare incognitum" of Wells (1957), has previously rarely if ever been sampled in this way. Therefore, since data on the variety of hosts this genus may occupy are presently lacking, we are justified in removing the genus from consideration at this time, and reranking the SDI and HEI columns accordingly (HEI—*Hiroa*, Table 2, A). The r_d value thus obtained

Table 2. A, rank-order comparisons between structural diversity (SDI) and indices for host exploitation (HEI), geographical distribution (GDI), and generic species richness (GSR); B, between indices for generic species richness, host exploitation and geographical distribution, and between geographical distribution, host exploitation and average generic age (AGA) of host corals.

A		HEI			GDI			GSR		
	SDI	World-wide	*-Hiroa*	Indo-Pac. *-Hiroa*	World-wide	*-Hiroa &-Hoekia*	Indo-Pac. *-Hiroa &-Hoekia*	World-wide	*-Hiroa*	Indo-Pac. *-Hiroa*
Ceratoconcha	10	5	4	—	4	3	—	6	5	—
Cantellius	9	10	9	7	8	6	5	10	9	7
Hiroa	8	2	—	—	1	—	—	2	—	—
Boscia	6.5	9	8	—	10	8	—	6	5	—
Creusia	6.5	7	7	5	5	4	3	6	5	4
Savignium	4.5	8	6	6	9	7	6	8	7	5
Nobia	4.5	6	5	4	6	5	4	9	8	6
Pyrgoma	3	4	3	3	3	2	2	2	1.5	1.5
Pyrgopsella	2	2	1.5	1.5	2	1	1	4	3	3
Hoekia	1	2	1.5	1.5	7	—	—	2	1.5	1.5
$r_d =$		.485	.738	.929	.037	.583	.672	.443	.638	.822
$p <$		.20	.05	.01	—	.20	.20	—	.10	.05

B		HEI	GDI			
	GSR	World-wide	World-wide	*-Hiroa & -Hoekia*	Indo-Pac.	Indo-Pac. *-Hiroa &-Hoekia*
Cantellius	10	10	8	6	7	5
Nobia	9	6	6	5	5	4
Savignium	8	8	9	7	8	6
Boscia	6	9	10	8	—	—
Ceratoconcha	6	5	4	3	—	—
Creusia	6	7	5	4	4	3
Pyrgopsella	4	2	2	1	2	1
Hiroa	2	2	1	—	1	—
Hoekia	2	2	7	—	6	—
Pyrgoma	2	4	3	2	3	2
$r_d =$		.83	.6	.655	.62	.77
$p <$		.01	.10	.10	.20	.20

		HEI		AGA	
	GDI	World-wide	*-Hoekia*	World-wide	"-0 age" corals
Boscia	10	9	8	7.5	8
Savignium	9	8	7	5	5.5
Cantellius	8	10	9	2	3
Hoekia	7	2	—	9	9
Nobia	6	6	5	5	7
Creusia	5	7	6	1	4
Ceratoconcha	4	5	4	7.5	5.5
Pyrgoma	3	4	3	3	1
Pyrgopsella	2	2	1.5	—	—
Hiroa	1	2	1.5	5	2
		.77	.929	.238	.629
		.05	.01	—	.10

is vastly improved (0.738, $p<0.05$), indicating a good correlation between being generalized in form and occupying of a wide variety of hosts.

Perusal of the HEI—*Hiroa* column (Table 2, A) indicates that the Caribbean genus *Ceratoconcha* is in good part responsible for the remaining "unexplained" variability. Since the Caribbean represents a distinct and relatively depauperate faunal province, *Ceratoconcha* too can legitimately be removed. This move would leave us with the cosmopolitan group (*Boscia*) and the Indo-Pacific group—*Hiroa*, and it can be observed from the ranks that an even more highly significant r_d would be anticipated. But since the correlation is already strong, and *Boscia* occurs primarily on ahermatypic corals, it would add little to our understanding. Therefore it would seem better to ask how the Indo-Pacific *Hiroa* group alone would stand. The r_d of 0.929 ($p<0.01$) is, considering the inadequacies of such biological data, astonishingly high.

Clearly generalized pyrgomatines occupy a greater variety of hosts than do specialists. Biologically this makes sense since the generalists, having made the principal adaptations necessary to inhabit living coral (ability of larvae to get through defenses of the coral, modification of growth form, cleaning mechanisms, etc.), are really specialists on corals, and therefore would be expected to occupy a wide spectrum of the available host types. It should also be noted that the composition of the reef coral dominants has, at least in the Indo-Pacific, not changed much since the Miocene, the epoch when the pyrgomatines first began to appear on the scene (Withers, 1929; Zullo, 1961; Baluk and Radwański 1967; Ross and Newman 1973). The coral barnacles are a relatively new group that underwent an explosive evolution. In being relatively new, the so-called unspecialized forms are actually dominants rather than simply early members of the subfamily. It is the model for the ancestors of the pyrgomatines, such as *Eoceratoconcha* in the Caribbean and *Hexacreusia* in the Eastern Pacific, both members of the Balanidae (Newman and Ladd, 1974a; Zullo and Beach, 1973 respectively), that are either extinct or refugial forms.

Structural Diversity and Geographical Distribution

Ross and Newman (1973: Figs. 2 & 3) have provided charts illustrating the distribution of pyrgomatine genera. The Cosmopolitan group, represented by *Boscia*, occupies shallow waters of the Caribbean and Western Pacific, and deeper waters of the Eastern Atlantic and Mediterranean. However, beyond its occurrence in southern Japan, it is replaced in shallow water in the bulk of the Indo-West Pacific by the diverse Indo-Pacific group; that is, only on the margin of this part of its range does it compete directly with the Indo-Pacific complex. In the Eastern Atlantic (and Mediterranean) it is found on ahermatypic corals in deeper water, but it surfaces again in the Caribbean where it inhabits hermatypic forms. The Caribbean however contains the remains of a once more widely distributed Tropical Atlantic group that was apparently more diverse in the past than it is today

(Newman and Ladd, 1974a), and *Boscia* has not diversified there. Competitive and other interactions probably account for the peculiarities in the distribution of the Cosmopolitan group, and certainly the historical aspects are highly relevant to understanding its present demise, but for present purposes it seems only necessary to emphasize that it differs from the tropical Atlantic and Indo-Pacific groups in these ways.

We have already noted that there is a good to excellent correlation between being structually generalized and exploiting a large variety of hosts. We can now ask whether or not there is a comparable correlation between structural diversity and geographical distribution. *A priori*, one might expect that a genus adapted to occupying a wide variety of hosts would be more widely distributed than one having a narrow host selection since the former, by virtue of exploiting different hosts, must extend through a wider range of gradients.

We are concerned with tropical marine organisms, distributed along the equatorial belt. The simplest measure of their geographical extent is latitude. Forms ranging widely latitudinally span a gradient in environmental conditions from the "center" to the edge of their latitudinal range, and those having wider ranges are probably adapted to a wider range of conditions than restricted forms. It would seem likely therefore, that they would also have relatively wider longitudinal distributions. The genera were ranked according to both their latitudinal and longitudinal extent. The resulting r_d of 0.798 ($p<0.05$) demonstrated a strong correlation between the extent of latitudinal and longitudinal distribution, on a worldwide basis. Thus a Geographical Distribution Index (GDI) can be formed by multiplying latitudinal by longitudinal range. For the robust rank-difference correlation, we did not correct for distortion imposed by the Mercator Projection.

It is now possible to compare SDI with geographical distribution, but the initial hypothesis, that generalized forms would enjoy wider distributions than specialized forms, fails to gain support on a worldwide basis (Table 2, A; GDI, worldwide). Perusal of the ranks indicates that two members of the Indo-Pacific group (*Hiroa* and *Hoekia*) are the principal misfits. Reasons for deleting *Hiroa* were given earlier. *Hoekia*, a form not only remarkable in being the most specialized with regard to shell characters, but also in being wholly parasitic, can reasonably be removed from the ranks in this case also. The result (Table 2, A, GDI-*Hiroa* and *Hoekia*), although much improved ($r_d=0.583$, $p<0.20$), is not compelling. Consideration of the Indo-Pacific situation alone (Table 2, A, GDI, Indo-Pac.—*Hiroa* & *Hoekia*) does not markedly improve the situation, and we are left without a strong correlation.

The distribution of a particular barnacle genus depends in good part on the distribution of the appropriate host or hosts, as well as the other factors mentioned above. Assuming the data available are sufficient and otherwise satisfactory, this may be the reason for the relatively poor fit. The distribution of corals also falls into patterns, and this aspect of the problem will be taken up briefly later.

Structural Diversity and Generic Species Richness

In the systematic section of their revision, Ross and Newman (1973) indicate the species assigned to each genus. Generalized genera tend to be more species rich (Table 2, A; GSR), but the r_d value is not significant ($p > 0.05$) on a worldwide basis. When *Hiroa*, again a misfit, is removed r_d jumps to 0.638 ($p < 0.10$). When the Indo-Pacific group alone, minus *Hiroa*, is treated, r_d becomes even larger (Table 2, A; GSR, Indo-Pacific—*Hiroa*). Clearly then, generalized genera not only tend to exploit a wider variety of hosts, and to some extent to occupy wider geographical ranges, than do highly specialized ones, but, as one might expect, they also have speciated to a greater degree. These three conditions go hand in hand; that is, wide geographical distribution and host exploitation provide greater opportunities for fragmentation of interbreeding populations through time, and hence speciation. Such opportunities have apparently been greater in the Indo-Pacific than in the Tropical Atlantic, at the generic as well as the specific level, since the latter province has been in a greater state of progressive geographical restriction from the time the coral barnacles first appeared there.

Generic Species Richness, Host Exploitation and Geographical Distribution

Since there is a strong correlation between generic species richness and structural diversity, it follows that generic species richness will probably hold a similar relationship to host exploitation and geographical distribution. Nonetheless, quantification of these relationships is necessary if direct comparisons are to be made. The ranks and r_d values are given in Table 2, B, where it will be observed on one hand that generic species richness holds a positive but not highly significant correlation with geographical distribution, a relationship which worsens when the Indo-Pacific group alone is considered. On the other hand, the correlation with host exploitation is highly significant (r_d 0.83, $p < 0.01$) on a worldwide basis.

Geographical Distribution and Host Exploitation

One might assume that the geographical range of a host genus would likely exceed that of the barnacle genus, and that this is indeed the case is readily illustrated in the Indo-Pacific, especially at the extremes where there are appropriate corals (Hawaiian Archipelago and Eastern Pacific) but no coral barnacles. It was noted above however, that structural diversity and geographical distribution, while correlated, were not strongly so. Generalized genera tend to be more widely distributed than specialists, and since they also occupy a wider variety of hosts, a stronger correlation would have been expected. The unexpectedly poor correlation is probably mainly due to distributional differences among coral host genera, but appropriate data, such as that forming the basis for the distributional study of the corals by Stehli and Wells (1971), are not readily available. So, while we know there is a greater concentration of host types at the centers of host distributions, we cannot readily determine how rarefaction of specific host genera, away from a center, influences the distribution of barnacle genera. However, since the most speciose barnacle genera definitely occupy a wider variety of hosts, there should be a good correlation between geographical extent and host exploitation.

A test of the relationship proves instructive (Table 2, B; GDI and HEI). On a worldwide basis, the correlation is good (r_d 0.77, $p<0.05$). A perusal of the ranks indicates that *Hoekia*, excluded on a previous occasion because it is the only wholly parasitic form, fits least well. When deleted, r_d jumps to 0.929 ($p<0.01$). Thus there is an excellent indication that genera occupying a wide variety of hosts are also widely distributed.

Average Generic Age and Geographical Distribution

Stehli and Wells (1971), show that not only do the number of coral genera decline as one moves away from centers of distribution, but that the widely distributed genera are of greater average generic age (AGA). That is, older coral genera are, in the main, more widely distributed, both latitudinally and longitudinally than younger ones. The "centers", where genera are most numerous, encompass regions where optimal conditions prevail. The wide-ranging genera then must be vagile, eurytopic forms (Newell, 1971). Since the coral barnacles depend upon coral as substrata, and those inhabiting a wide variety of coral hosts tend to be more widely distributed than others, it might be expected that they would be exploiting corals of greater generic age.

Unfortunately Stehli and Wells (1971) do not identify the coral genera involved in their analysis, so a direct comparison cannot be made. However, we have compiled a list of the corals inhabited by various barnacle genera and utilizing Wells (1956), have assigned their ages. The average generic age of the hosts (AGA) for each barnacle genus is then calculated and compared to the geographical distribution indices for each barnacle genus (Table 2, B). An inspection of the ranks suggests that if there is a correlation at all, it is positive but very weak.

Stehli and Wells (1971) consider the problem of corals lacking a fossil record; that is, those of "0" age. Since as many as 20 percent of the coral genera in the Indo-Pacific center have 0 ages, if a fair proportion were actually a good deal older, the AGA pattern would be significantly altered. Since 26 percent of the occurrences of coral barnacles fall among coral genera of 0 age, the same difficulty would influence the AGA of the corals playing host to the barnacles. Thus it seems appropriate to delete the 0 age hosts and see how the resulting AGA values compare with the GDI rank. The resulting r_d (Table 2, B; 0.629, $p<0.10$) does indeed suggest to one that the wide-ranging barnacle genera tend to exploit corals of high average generic age.

As already mentioned, the association with corals apparently began in the Miocene and mid-ranked forms such as *Savignium* and *Nobia* of the Indo-Pacific appeared during the same epoch. Even though diversification, at least in the Indo-Pacific, was relatively rapid, generalized forms must still have been first on the scene and therefore would have been in a position to invade susceptible corals before the more advanced forms arrived. We have already noted significant correlations between being generalized in structure, in exploiting of a wide variety of hosts, and in being geographically widely distributed. It would then seem likely that the corals inhabited would have similar attributes. If such widely distributed coral genera are geologically older it follows that generalized barnacles should be found on corals of greater average generic age than should specialized ones. While there is a suggestion that this is the case in the foregoing comparison, further documentation awaits better knowledge of the distributions of both coral and barnacle genera.

Summary and Conclusions

Correlations covered in the preceding sections are summarized in Figure 2, A. While the values selected from the foregoing tables were chosen as those expressing a relationship, they are not necessarily the largest. For example, SDI-HEI had an r_d of 0.485 ($p<0.20$) on a worldwise basis, of 0.738 ($p<0.05$) if *Hiroa* was removed, and of 0.929 ($p<0.01$) if only the Indo-Pacific representatives minus *Hiroa* were considered. The second value is sufficient to allow one to generalize. Similarly, the SDI-GDI r_d of 0.583 ($p<0.20$), worldwide minus *Hiroa* and *Hoekia*, while not as high as the same relationship (0.672, $p<0.20$) for the Indo-Pacific minus the same genera, also suggests correlation. Although the table forms an overall summary, the interrelationships are not easily visualized.

Since r_d^2 provides an approximate percentage of the variation of either variable explained by its correlate, 100-r_d^2 is an estimate of that not explained. If all 100-r_d^2 values were zero, correlations would be perfect and could be represented graphically by the same point in space. Conversely, if all were 100 (entirely uncorrelated), they would be equally separated from each other in space, and since there are four indices, the geometrical figure formed would be an isometric tetrahedron. However, in practice, values fall somewhere between zero and 100, and provided they are relatively similar, form a smaller anisometric tetrahedron. Such a figure graphically illustrates not only the degree of departure from a perfect correlation, but allows one to more readily visualize the interrelationship between parameters.

A tetrahedron has three dimensions, but in this particular case (Fig. 2, B), it can be closely approximated in two. The lines formed by points SD, GSR and GD are proportional to their actual values and form the base of the tetrahedron. However, to place point HE, the apex of the tetrahedron, lengths SD-HE, GSR-HE and GD-HE were drawn with a compass as radii centering on SD, GSR and GD respectively, and the center of the small three-sided figure formed was then taken to represent HE. Thus, in completing the tetrahedron, GSR-HE and GD-HE are slightly shorter and SD-HE is slightly longer than their actual lengths (~5 percent).

A

	HEI	GDI	GSR
SDI	World *-Hiroa* 0.738 (p<.05)	World *-Hiroa & -Hoekia* 0.583 (p<.20)	Indo-Pac. *-Hiroa* 0.822 (p<.05)
HEI	———	Worldwide 0.77 (p<.05)	Worldwide 0.83 (p<.01)
GDI	———	———	Worldwide 0.60 (p<.10)

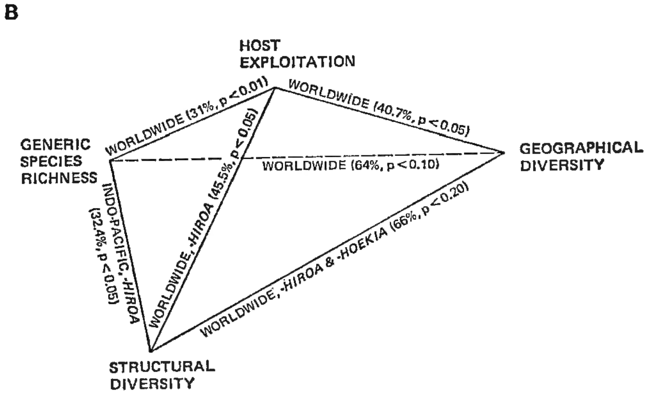

Fig. 2. A, rank-correlation coefficients selected from Table 2 utilized in constructing the accompanying geometric figure; B, resulting anisometric tetrahedron, based upon percentage departure $(100-r_d{}^2)$ from a perfect correlation, illustrating the interrelationships between structural diversity, generic species richness, host exploitation and geographical distribution.

In viewing Figure 2, B, it will be noted that the back side (that formed by GSR, HE and GD) holds the most encompassing generalization; species rich genera exploit a greater variety of hosts and have greater geographical ranges than less species rich genera, on a worldwide basis. Indeed, this is what would have been expected. The interesting thing to look at now is how these three parameters correlate with structural diversity.

A priori, one might expect that considerable specialization would be necessary in order to exploit the intracoralline habitat to a significant degree. If true, one might expect the more advanced pyrgomatines to exploit the widest variety of hosts, and, concomitantly be more species rich and enjoy wider geographical ranges than the more generalized members of the group. This turns out not to be the case, just the reverse being generally true. The reason for this is quite clear. The pyrgomatines constitute a tightly defined group of coral-inhabiting barnacles, the definition of which excludes genera that in many respects are more generalized than the so-called generalized members of the subfamily. Thus, the so-called generalized pyrgomatines are actually relatively specialized. The so-called specialists then are extreme specialists which, rather than having acquired adaptations allowing them to exploit a larger proportion of the available host types, the portion already occupied by the so-called generalists, have invaded otherwise inaccessible small portions of the available habitats.

Again consulting the diagram (Fig. 2, B), with these points in mind, it can be seen that the so-called structurally generalized forms exploit a wider variety of hosts than do the specialists, on a worldwide basis (*Hiroa* deleted). Concomitantly, they have wider geographical ranges (*Hiroa* and *Hoekia* deleted) and, for the Indo-Pacific (*Hiroa* deleted) are more speciose. The deletions, as discussed earlier, have been deemed appropriate where necessary to achieve strong correlations; *Hiroa* is a recently discovered relatively generalized form known from a single locality and host, *Hoekia* is highly specialized (the only wholly parasitic member of the subfamily) and happens to enjoy a remarkably wide geographical range. The cosmopolitan group for the most part occurs on ahermatypic corals in deeper water. The Caribbean group represents an arm of the historically more widely distributed tropical Atlantic coral biota that supported a greater diversity of coral barnacles in the past than it does today and as such would not likely express diversity trends entirely parallel to the Indo-West Pacific.

The value of these generalities is no doubt in some respects limited by the quantity of the available data, the way these data have been handled, and the extent of error from all sources that were unavoidably included. The structural diversity indices have been derived from the most recent phylogenetic scheme and, while we do not expect it to change drastically in the future, with increasing knowledge some change is inevitable. Generic species richness will undoubtedly change, but one would expect that proportionality would remain much the same. Host exploitation on the other hand needs considerable work both in weeding out misidentifications and filling in gaps, and, in either case, improvement depends on better knowledge of corals.

The most serious problem seems to us to be geographical distribution. The difficulty with *Hiroa* has already confronted us—a recently discovered type, the location of which is on the outer edge of the Indo-Malayan center of distribution. The recent marked range extension for *Hoekia*, lack of knowledge of forms from French Oceania in the South Pacific and Grand Chagos in the Indian Ocean, and the apparent occurrence of coral barnacles from Western Australia (Wilson, pers. com.), all point to the likelihood of considerable improvement in our knowledge of the distribution of these organisms. Withstanding such shortcomings and the undoubted refinements to be made in the relationships presented here, it is clear that coral barnacles in their spectacular evolution and diversification reflect general ecological and evolutionary principles probably applicable to other reef organisms, despite their being obligate commensals.

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