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CORALLITE VARIATION IN PORITES AND THE SPECIES PROBLEM IN CORALS

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ABSTRACT

Corallite variation was examined in 140 Porites colonies, collected at Discovery Bay, Jamaica, by the quantitative study of 20 corallite characters shown to be free of most environmental influences. Cluster analysis revealed the existence of several concentrations of morphologically similar specimens, some of which corresponded to Porites species as traditionally defined. These clusters were not distinct, however, but were connected by many intermediate forms. It is suggested that the complex nature of variation in this coral genus and others is a direct consequence of the diversifying selection pressures exerted upon coral populations by their environment. Taxonomic difficulties among the Scleractinia at the species level are thus not merely the result of inadequate study, but reflect fundamental, intrinsic genecological properties of coral populations.

KEY WORDS: Coral, Ecology, Jamaica, Numerical Taxonomy, Porites, Reef, Scleractinia, Species, Variation

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Introduction

The taxonomy of reef-building corals is based primarily on the morphology of the skeletal structures associated with the individual polyp, because these calcium carbonate structures, known collectively as the corallite, require no special preservation, are easily studied, and provide a direct comparison with the fossil record. Taxonomic distinctions are sometimes based on aspects of colony form. This approach, though convenient for quick identifications in the field, is less satisfactory for precise systematic work because colony traits are sometimes known to vary greatly in response to environmental factors (1).

As the result of over a century of painstaking collecting and observation, approximately 450 genera of Scleractinia have been described (2). Although there are conflicting views as to how these genera are to be classified into families and suborders (3-6), the enumeration and characterization of the genera themselves is widely accepted. At the species level, by contrast, there still remains much uncertainty and controversy (7). There are two possible reasons for this confusion:

1. Standard methods of corallite observation and description have been inadequate; more quantitative study is needed, with special attention to the effect of ecological factors on corallite variation.

2. The pattern of genetic variation in coral populations is inherently so complex and subtle that it precludes any simple taxonomic resolution at the subgeneric level, regardless of future refinements in observation or methodology.

In this paper I present the results of a detailed, quantitative study of corallite variation in Jamaican representatives of Porites, a common, cosmopolitan genus whose taxonomy at the specific level has been debated for many years, in order to explore some aspects of the species problem in corals. Porites was recognized and described by one of the earliest students of zoophytes (8), and was elevated to generic status in 1807 (9). Goreau and Wells (10) listed five species as commonly occurring in Jamaica: P. astreoides, P. branneri, P. furcata, P. porites, and P. divaricata, but some authors (11, 12) have considered the latter two or three as varieties of a single species.

MethodsCollection of Specimens

Field investigations were carried out at seven study sites at Discovery Bay, Jamaica (13). These sites represented a wide range of reef habitats, with very different conditions of illumination, wave energy, and sediment resuspension. Sites 1-3 were located in 3.0, 9.0, and 0.3 meters (m) of water in the sheltered bay. Sites 4-7 were situated at depths of 4.6, 9.8, 18.3, and 27.4 m on the exposed fore-reef terrace and escarpment. At each site I surveyed the bottom in contiguous 0.5 m² quadrats along an arbitrary transect line. An average of 13 quadrats were covered at each site. Every time I encountered a Porites colony in a quadrat, I made note of its position on the substrate (slope and exposure) and collected a fragment of the corallum for further study. A total of 45.5 m² of reef bottom were thoroughly searched; 140 Porites specimens were collected.

Corallite Characters

The intricacy, irregularity, and small size of Porites corallites have frustrated many coral taxonomists (14). The methods of numerical taxonomy (15) provide a means of coping with this complexity. My approach was to identify as many quantifiable characters of the Porites corallites as possible, subject only to the restriction that these traits be logically uncorrelated with each other and invariant within any one colony.

After a period of trial and error a workable list of 20 characters was obtained (Table 1). Of these, 13 were directly-measurable, continuous characters. For the other seven the character states were arbitrarily defined and assigned integer code numbers. All observations were made on the upward-facing, planar or slightly convex surfaces of bleached skeletal fragments, using a 7-30 x binocular microscope fitted with an ocular micrometer. The angle through which the focus knob had to be turned to bring pairs of structures into focus was used as a measure of the vertical distance separating them.

Statistical Analysis

Cluster analysis provides an objective method for assessing the morphological similarities between specimens. Each colony is viewed as a point in multidimensional space whose coordinates are the specimen's standardized scores for the 20 corallite characters measured on it. The

Euclidean distance between all pairs is calculated, and the most similar corals are then sequentially entered into a tree diagram and are connected with their neighbors at a distance from the origin proportional to the Euclidean distance between them. Groups of specimens are connected at a distance to reflect the weighted mean of the distances between their constituent specimens. Calculations were performed on the Yale Computer Center's IBM 370/158 using the BMDP2M program developed at the U.C.L.A. Health Sciences Computing Facility (16).

Results

The average-linkage dendrogram of 140 *Porites* specimens is shown in Figure 1. Each horizontal line represents a different specimen; those that are joined together at the smallest distance (furthest to the right) represent the most similar corals. Two major conclusions can be drawn from inspection of the dendrogram:

1. Variation is nearly continuous; there are few sharp morphological discontinuities. This is evidenced by the repeated stepwise amalgamation pattern. With each additional specimen a slightly different corallite morphology is encountered, thus each is connected to the tree at a slightly greater distance from the origin.

2. Within this intergrading series of morphologies there do exist several concentrations of more similar specimens. If we arbitrarily draw a line across the dendrogram at a distance of 3.7 (indicated by an arrow on the distance axis), then six major clusters of specimens, termed phenons, are established. These phenons are marked off in brackets to the right of the tree. Typical corallites from three of these phenons are shown in Figure 2. Note that many specimens do not fit into any cluster at this level of similarity and that the size and number of clusters depend entirely on where one chooses to draw the phenon line.

Table 1. List of Corallite Characters

- | | |
|--|---|
| 1. shape of cup (calice):
1=circular 2=angular 3=sharply polygonal | 11. septal linearity:
1=straight
2=somewhat bent
3=sharply bent or zig-zagged |
| 2. maximum cup diameter, including wall width;
mean of 10 observations | 12. mean number of septa meeting or fusing at
the center of the cup |
| 3. cup size: average cup area, calculated from
cup diameter minus wall width | 13. septal ornamentation:
1=none
2=less than five teeth per septum
3=five or more teeth per septum |
| 4. cup symmetry: ratio of maximum to minimum cup
diameter | 14. depth of septa (at their midpoint) below
the highest point of the corallite surface |
| 5. cup diameter variability: variance of dia-
meter divided by mean | 15. mean width of septa at their midpoint |
| 6. wall (thecal) structure:
1=reticulate; loose network of trabeculae
2=open; more open space than skeleton
3=spongy; trabeculae largely consolidated
4=solid; virtually no gaps in wall | 16. number of pali (pillars at the inner edges
of the septa) |
| 7. wall profile, discounting irregularities due
to individual trabeculae:
1=level, even
2=somewhat uneven
3=with distinct peaks and valleys | 17. paler variability: variance in number of
pali divided by mean |
| 8. maximum width of wall between adjacent cups | 18. depth of pali below the highest point of
the corallite surface |
| 9. shape of septa:
1=tapering toward center of cup
2=uniform width
3=tapering outward | 19. depth of the columella (axial pillar) below
the highest point of the corallite surface |
| 10. symmetry of septal pattern:
1=totally irregular
2=partly or superficially regular
3=regular, consistent, symmetrical | 20. height of the columella above its lateral
attachments |

Discussion

Sources of Corallite Variation

Are the morphological variations in Porites corallite structure genetically programmed or environmentally induced? The usual way to distinguish between these two sources of variation is to move individuals experimentally from different environments to uniform conditions and those from one environment to different conditions, and observe the phenotypic response, if any (17). This experimental approach can be circumvented, given what we know about the provenance of the Porites specimens and their colonial growth habit. It can be deduced that the observed pattern of variation has an overwhelming genetic component. Three lines of evidence lead to this conclusion:

1. If we assume that most coral colonies arose from a single planula and are thus genetically homogeneous, then by the exclusion of characters with a significant degree of intracolony variation we have concomitantly eliminated those traits that are most strongly affected by environmental factors (18). (Some traits in Table 1 do show intracolony variability, but for these characters the variants are randomly interspersed across the colony surface and are clearly not responding to changing micro-environmental conditions about the corallum.)
2. Corals from very different environments may have very similar corallite structure. For example, the 19 very similar specimens in the middle of phenon 1 that are joined together at a distance of 3.0 turn out to have originated from six different study sites, spanning a depth range of 27.1 m. For so similar a corallite configuration to have arisen from such disparate environments suggests a strong degree of genetic control over corallite architecture.
3. Specimens from very similar environments often have radically different corallite morphologies. Several pairs of corals were found together in the same quadrat and on substrates with similar slope and exposure. Members of these pairs are marked on the dendrogram with the same letter of the alphabet. Corallite differences between these corals growing side by side under nearly identical conditions can only be due to genetic differences.

Thus I conclude that the pattern of variation shown in the dendrogram reflects primarily genetic differences between these Porites colonies. It appears therefore that there is a continuum of genetic variation in these Jamaican poritids, but that some forms are found in the population at higher frequencies than others, leading to clusters of more similar specimens. These clusters have been given the rank of

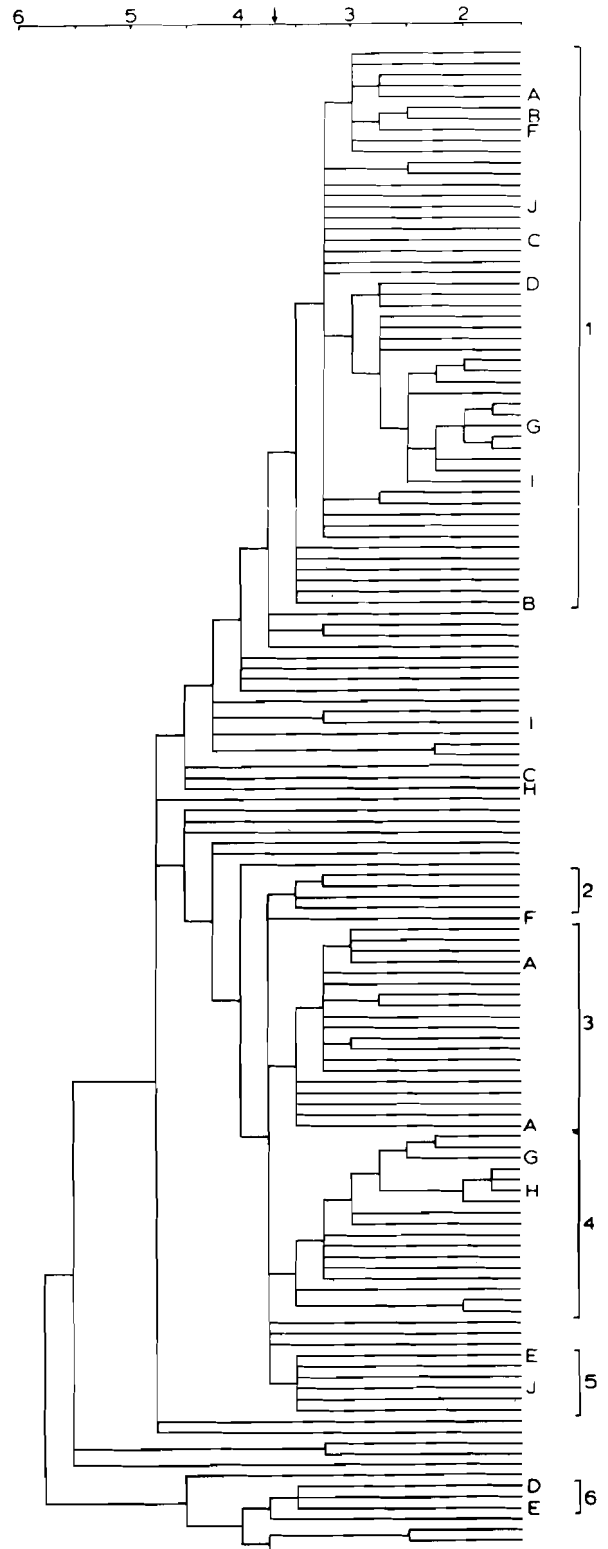


Figure 1. Dendrogram of Jamaican Porites specimens based on 20 corallite characters. Axis at top indicates amalgamation distance. See text for details.

species by some authors. Phenon 1 in the dendrogram, for instance, clearly contains *P. astreoides* colonies. Phenon 4 contains specimens that might be called *P. furcata*. But between these six clusters there exist many intermediate forms, which constitute about 26% of the population.

Causes of the Observed Pattern of Variation

Little is known about the genetic and population structure of corals (19), thus it is difficult to interpret these results by considering the Scleractinia alone. Terrestrial plants, however, have been well studied in this regard, and share many ecological characteristics with corals:

1. They are sessile as adults, and therefore cannot take refuge in times of stress.
2. To facilitate gas exchange and the interception of light their tissues are arrayed in thin, exposed layers on elaborate supporting structures. This makes them particularly vulnerable to the vicissitudes of the environment.
3. They live in heterogeneous, topographically complex communities. Two individuals growing only a short distance apart may therefore experience very different micro-environments.
4. They have little control over where their propagules eventually land and take root.

The first three conditions undoubtedly apply to corals as well. The question of the dispersal of offspring is more complex. In the laboratory, coral planulae show the ability to select settling sites (20), but it has also been argued that such larvae may not often have the opportunity to actually exercise their habitat preferences under natural conditions (21).

All these factors taken together indicate that both plants or corals in any given population potentially encounter very different environments, and may feel the impact of these differences pronouncedly. In other words, their populations are subject to intense diversifying selection. In plants it has been demonstrated that such conditions can lead to complicated and unexpected patterns of genetic variation, including, for example, the evolution of genetically distinct races or ecotypes on the highly localized scale of meters or centimeters (22-24).

We may therefore expect that in corals, too, there are opportunities for specialization and differentiation within potentially interbreeding populations. Thus when we examine variation in corals below the genus level we may well encounter very complex and subtle patterns quite unlike the discrete, disjunct variation that is indicative of "good" species.

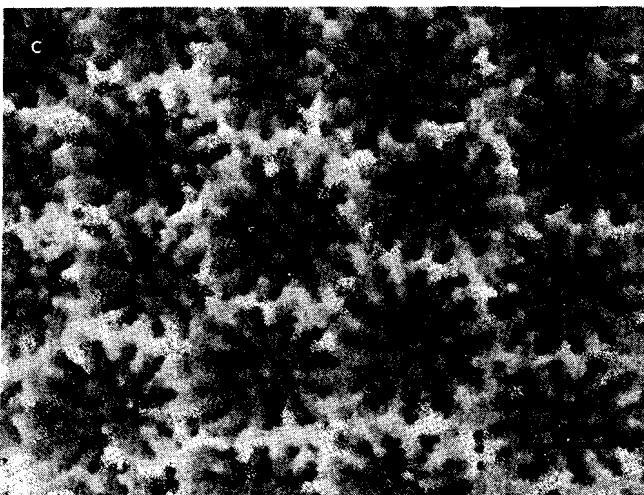
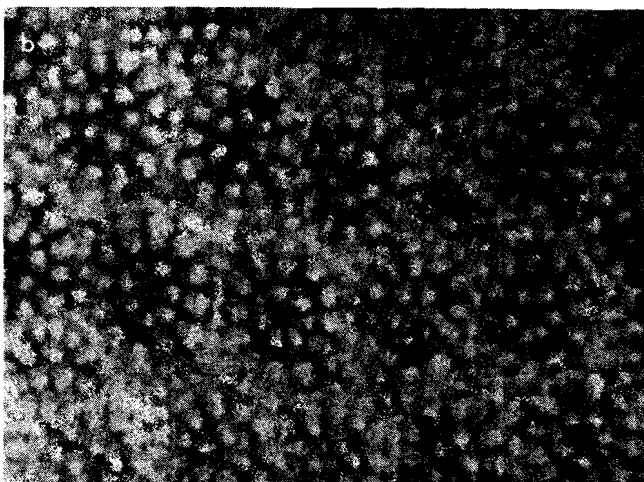
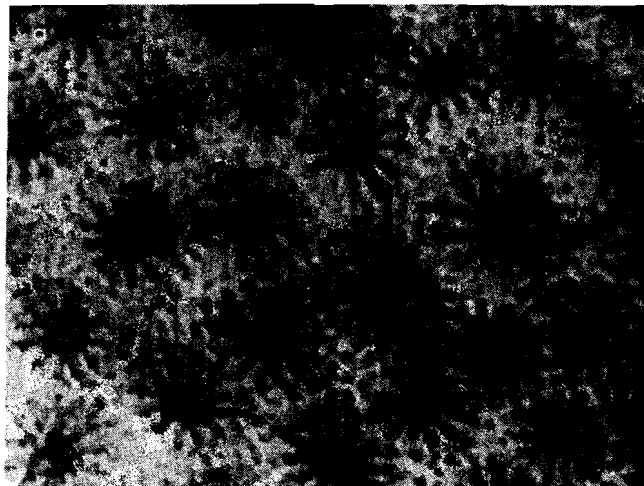


Figure 2a,b,c. Representative corallites from phenons 1, 4, and 5, respectively, illustrating the range of variation. Scale bar is 1 mm long.

Other patterns of variation

The pattern of variation seen in Porites is not the only one that might be expected. Genetic differentiation is just one mechanism by which populations can adapt to a heterogeneous environment. Another is phenotypic plasticity, the mechanism that allows one genotype to produce various phenotypes in response to different environmental conditions (25). This "strategy" is seen in many faviid corals, among which corallite structure is strongly influenced by the environment (26-28). It may therefore be that different groups of scleractinians have evolved contrasting adaptive solutions to the patchiness and uncertainty of the reef environment.

Conclusion

A detailed, quantitative study of corallite variation in Porites, after the exclusion of most environmentally induced variability, did not provide any easy solution to the taxonomy of the genus, but only revealed a greater level of taxonomic complexity. I suggest that in this coral genus, and perhaps in many others as well, the heterogeneity of the environment and the attendant diversifying forces of natural selection have produced an inherently complex pattern of genetic variation that cannot be resolved into a simple classificatory scheme. The species problem in corals is therefore not necessarily an artifact of poor methodology or insufficient data, but may reflect intrinsic genetic and ecological properties of coral populations.

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