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Shape Variation in Hydractiniid Hydroids

NEIL W. BLACKSTONE[1] AND LEO W. BUSS[1,2]

[1]*Department of Biology, and* [2]*Department of Geology and Geophysics, Yale University, New Haven, Connecticut 06511*

Abstract. Colonies of hydractiniid hydroids consist of feeding polyps connected by a common gastrovascular system. The gastrovascular system consists of stolons, which enclose gastrovascular canals. Stolons may be fused into a stolonal mat or extend from the periphery of the colony. *Hydractinia* forms a stolonal mat early in colony development; *Podocoryne,* on the other hand, does not. To facilitate comparisons of these taxa, we propose a simple shape metric, $perimeter/\sqrt{area}$, and show that this measure: (1) correlates closely with relative amounts of peripheral stolon and stolonal mat structures in *Hydractinia,* (2) permits analyses of within- and between-species variation of growth morphology in *Podocoryne* and *Hydractinia,* and (3) allows quantitative analysis of breeding studies of *Hydractinia,* both before and after stolonal mat formation in the progeny.

Introduction

Hydractiniid hydroids encrust hard substrata in the sea. *Hydractinia echinata* and related species are commonly found on the shells of hermit crabs and often exhibit a species-specific correlation with host hermit crabs (Buss and Yund, 1989; Cunningham *et al.,* in press). *Podocoryne carnea* also encrust hermit crab shells, but commonly inhabit other substrata as well (Edwards, 1972; Mills, 1976). Colony development in both taxa begins with the metamorphosis of the planula larvae into a primary polyp. Runner-like stolons extend from the primary polyp. Stolons encase fluid-filled, gastrovascular canals that are continuous with the gastrovascular cavity of the polyp. *Podocoryne* continues to develop in this way, *i.e.,* by lineal extension of the stolons, initiation of new stolon tips, and iteration of feeding polyps on the stolons (Braverman, 1963; McFadden, 1986). Stolons in *Hydractinia,* however, quickly fuse to form a continuous stolonal mat, which shows sheet-like growth, and from which extend varying amounts of peripheral stolons (McFadden *et al.,* 1984; Blackstone and Yund, 1989; Buss and Grosberg, 1990). Figure 1 provides rough schemata of the differences in form between these taxa.

While morphological variation within each taxon has been compared and related to ecological characteristics (*e.g.,* competitive ability; see McFadden *et al.,* 1984; McFadden, 1986; Yund, 1987; Buss and Grosberg, 1990), quantitative comparisons of between-taxa variation have been hampered by the differences in growth form, *i.e.,* the presence of a stolonal mat in *Hydractinia* and its absence in *Podocoryne.* For instance, competitive ability among strains of *Hydractinia* has been shown to correlate with relative amounts of peripheral stolon and stolonal mat structures (measured using several methods, see McFadden *et al.,* 1984; Yund, 1987; Buss and Grosberg, 1990), but such measures cannot be applied to *Podocoryne.*

To facilitate comparisons of biological traits between *Podocoryne* and *Hydractinia,* we propose a simple measure of morphology that can be used in both taxa. We show that this measure correlates with ratios of peripheral stolon and stolonal mat structures in *Hydractinia,* and we use this measure to examine morphological variation and its genetic basis both between and within *Podocoryne* and *Hydractinia.* Finally, we relate this variation to ecological, evolutionary, and developmental aspects of these species and discuss the relevance to other clonal taxa as well.

Materials and Methods

Growth morphology and shape

We suggest treating hydractiniid hydroids as geometric shapes for purposes of comparison. We prefer Bookstein's

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(1978: p. 8) definition: ". . . a shape is an outline-with-landmarks from which all information about position, scale, and orientation has been drained," with the qualification that hydroid colonies have no reliable morphological landmarks. Further, the aspects of hydractiniid growth morphology of particular interest are essentially two-dimensional, comprising those portions of the colony that adhere to the substratum. Although there are sophisticated techniques available for the analysis of two-dimensional shapes-without-landmarks (*e.g.,* Lohman, 1983; Ferson *et al.,* 1985), we will take a simpler approach. The terms previously used to categorize hydractiniid growth morphology (many peripheral stolons = "net type," few peripheral stolons = "mat type," see Hauenschild, 1954) point out an intuitively obvious correlation between two-dimensional growth morphology and shape. Colonies with few peripheral stolons often show approximately circular growth forms, while colonies with many peripheral stolons exhibit more irregular shapes (Fig. 1).

An appropriate "size-free" metric to quantify these differences in shape is $perimeter/\sqrt{area}$ (*cf.,* Gould, 1973; Patton, 1975). We point out several properties of this measure, by way of introducing it to morphological studies of encrusting clonal organisms. First, regardless of scale, this measure is constant for a given geometric shape. For instance, this measure will equal $2\sqrt{\pi}$ for a circle, 4 for a square, $\approx$4.5 for an equilateral triangle, $\approx$5.4 for a "first-aid" sign, $\approx$5.7 for a cross (length of the long arm is twice that of the three short arms), and so on. In each case, these values are constant regardless of the actual size of the object as long as the same units are used to measure both perimeter and area. Second, while the same geometric shapes will have similar $perimeter/\sqrt{area}$ values, shapes with the same $perimeter/\sqrt{area}$ need not be the same. In fact, for encrusting clonal organisms, no two shapes are likely to be the same, yet many may have similar $perimeter/\sqrt{area}$ values. This shape metric thus only assesses the degree of circularity of a shape. Shapes with values close to $2\sqrt{\pi}$ approach perfect circularity, while highly non-circular shapes have much larger values. Third, $perimeter/\sqrt{area}$ has a minimum at $2\sqrt{\pi}$; possible values thus have a lower bound, and their distributions may be skewed. Note that this is not unusual; most morphometric measurements have a lower bound at zero and thus may form skewed distributions. Regardless of the lower bound (0 or $2\sqrt{\pi}$), a log-transformation usually provides distributions suitable for parametric analysis (see Sokal and Rohlf, 1981).

The utility of this measure may be visualized by comparing a plot of perimeter and area for two sibling *Hydractinia* colonies (Fig. 2) grown from primary polyps under standard conditions (see McFadden *et al.,* 1984). While the perimeter *versus* area trajectories fluctuate as stolons branch and fuse, it is clear that the colony with a greater amount of stolons projecting from the center has a larger perimeter for a given area and larger $perimeter/\sqrt{area}$ values. To assess quantitatively the capacity of this shape metric to assay the amount of peripheral stolons, we measured the correlation between $perimeter/\sqrt{area}$ and peripheral stolon development for the 242 *Hydractinia* colonies used in a breeding study (see protocol below). At age 50 days, each colony was measured using a digital image analysis system. Briefly, an Eyecom II camera attached to a Wild Makroskop was used to project each colony onto a black-and-white monitor (640×480 pixels; note that the pixels are orthogonal and that the length of a pixel is the same in either direction). Points on the video image of each colony were recorded with a digitizing tablet interfaced with a DEC PDP-11 minicomputer. The outline of each colony was traced with points at 5 pixel intervals, and the perimeter and area were computed. The outline of the stolonal mat, *i.e.,* the fused stolons (see Fig. 1), was also traced, and the perimeter and area were measured. Scales ranged from 150 pixels/mm for the smallest colonies to 25 pixels/mm for the largest colonies. Over this range of observation, these colonies are not fractal, *i.e.,* they do possess a characteristic scale and do not show self-similarity over the different scales of observation employed here (although self-similarity may be apparent using other scales of observation). Thus, while smaller colonies were measured with slightly greater resolution, this did not bias the results in a systematic fashion. Data were transferred to an IBM-PC and uploaded to an IBM 3083 mainframe where analysis was done using SAS software.

Comparing peripheral stolon development to colony shape entails methodologic problems. Logical measures of peripheral stolon development involve a measure of the total size of the colony divided by the size of the stolonal mat (*e.g.,* total colony perimeter/stolonal mat perimeter and total colony area/stolonal mat area). Given the nature of colony growth (*i.e.,* peripheral stolons projecting from a central area of stolonal mat, Fig. 1), the extent to which these ratios are greater than 1 will measure the amount of peripheral stolons. A straightforward procedure would be to correlate these ratios to the total perimeter divided by the square root of the total area (*i.e.,* the shape metric). However, this could result in autocorrelation, because both ratios necessarily contain measures of the overall size of the colony (either total perimeter or total area). We measured these correlations and then assessed the effects of autocorrelation by adjusting the correlated ratios to remove similar variables from each. For instance, the correlation of the ratio, colony perimeter/stolonal mat perimeter, to the ratio, $perimeter/\sqrt{area}$, can

be considered equivalent to the correlation of stolonal mat perimeter to $\sqrt{area}$ if there are no effects of autocorrelation. Further, we considered the biological meaning of correlations between stolonal mat size and total colony size and whether these correlations support our interpretation of the shape metric. Spearman's coefficient of rank correlation (r_s) was used; this coefficient is less sensitive to the statistical pecularities of ratios than parametric correlation coefficients (see Sokal and Rohlf, 1981), although here both coefficients were similar for all correlations.

Shape variation in Podocoryne *and* Hydractinia

The *perimeter/*$\sqrt{area}$ measure was used to compare morphological variation within and between field-collected colonies of *Podocoryne* and *Hydractinia* using the technique of clonal repeatibility, *i.e.,* comparing clonal replicates of the same colony to gauge broad-sense heritability (Falconer, 1981). Colonies were collected from an intertidal site near Guilford, Connecticut, where *Podocoryne carnea* and *Hydractinia symbiolongicarpus,* a sibling species of *H. echinata,* commonly co-occur (Buss and Yund, 1989), although *Podocoryne* is much less abundant than *Hydractinia.* When reproductive polyps are present, these species can be easily distinguished: *Podocoryne* produces free-swimming medusae, while *Hydractinia* lacks a medusoid stage and produces fixed gonophores (Mills, 1976). Using a dissecting microscope, *Podocoryne* colonies were identified from large collections of all hydroid-bearing hermit crab shells. Relatively few colonies contained reproductive polyps; hence, tentative identifications were made on the basis of general patterns of colony appearance (in this area, *Podocoryne* has few spines and usually co-occurs with algal epibionts) and feeding polyp morphology (in this area, *Podocoryne* tends to have smaller polyps, a more pronounced hypostome, and shorter, more tapered tentacles). In this way, 60 colonies were tentatively identified as *Podocoryne* and were labelled with numbered bee tags attached with cyanoacrylate adhesive. Colonies were maintained in 40-liter aquaria with undergravel filters (20 colonies per tank) at 16°C. Colonies were fed 3-day-old brine shrimp nauplii (also grown at 16°C) every other day, and 25% of the water was changed twice a week. In 1–2 weeks all colonies were reproductive (tentative identifications were correct in all cases). Medusae from each colony were isolated and raised in finger bowls at 16°C. Each day, medusae were examined under a dissecting microscope, fed brine shrimp, and transferred to fresh seawater. Medusae were raised to sexual maturity (7–14 days), and the sex of the parent colony was determined by the morphology of the gonads (Rees, 1941; Edwards, 1972; identity as *P. carnea* was also verified by examining the medusae, see Edwards, 1972; Mills, 1976). From the original 60 colonies, 10 male and 5 female colonies were selected using a pseudo-random number generator. Sixty *Hydractinia* colonies were haphazardly collected from the same site and maintained in the same fashion. Compared to *Podocoryne, Hydractinia* requires more time to mature (*cf.* Hauenschild, 1956; Braverman, 1963), but within two months all colonies were fully reproductive, whereupon they were sexed, labelled, and 10 male and 5 female colonies were selected with a pseudo-random number generator. Previous investigations (McFadden *et al.,* 1984; Buss and Grosberg, 1990) have shown that colony morphology does not differ on the basis of sex; nevertheless, equal numbers of each sex from each species were included in this study.

For morphological comparisons, colonies were surgically explanted onto 22 mm^2 glass cover slips and held in place with loops of thread until attachment whereupon the threads were removed (see McFadden *et al.,* 1984; explants of 3–5 feeding polyps were used). Because of the work involved, comparisons were made using five field-collected colonies of each species at a time. Five explants (hereafter "replicates") for each of the five field-collected colonies (hereafter "strains") for both *Podocoryne* and *Hydractinia* (hereafter "species") were grown in a floating rack at 16°C. Three "racks" were used over a two-month period; rack is thus a proxy for time effects. Each rack consisted of two side-by-side rows of slots; cover slips were arranged so that the five replicates for each strain occupied consecutive slots; strains of each species were randomly paired, alternating right and left sides. The formal analysis thus consists of a four-level nested analysis of variance (see Sokal and Rohlf, 1981). Replicates are nested within strains, which are nested within species, which are nested within racks. Such an analysis accounts for all sources of variation except position within racks. Position effects can be assessed by designating five positions within each rack; each position then contains the replicates from a pair of *Podocoryne* and *Hydractinia* strains. The analysis then becomes replicates within species within positions within racks. Outcome variables were analyzed in both ways.

Using the above protocols, *perimeter/*$\sqrt{area}$ measures were taken, and counts of polyps and total area measures were also recorded. Variables were measured at 7 and 14 days after explanting; specific growth rates (see Blackstone, 1987; Blackstone and Yund, 1989) for polyp (*polyp/polyp-day*) and area (mm^2/mm^2*-day*) were also calculated for this interval. Each rate was calculated by increment in number or area (for polyp number and total area respectively) per time increment per initial number or area. While technically "specific" refers to "divided by mass," any measure of size can be used, provided the same units are used in the numerator and denominator, since a specific growth rate has units of 1/time.

Breeding studies

While studies of clonal repeatibility can establish broad-sense heritabilities for a trait, breeding studies can provide further insight into the nature of the genetic variation underlying a trait (Falconer, 1981). With the same 5 female and 10 male *Hydractinia* colonies used above, 10 crosses (2 males per female) were designated using a pseudo-random number generator, and additional mating experiments were done to insure that all individuals belonged to the same species (see Buss and Yund, 1989). Matings were carried out every several days for a month. Pairs of male and female colonies were isolated in the dark overnight; morning light triggered gamete release (see Yund *et al.*, 1987, and references therein). Embryos were transferred to fresh seawater and kept for 3–4 days with a daily water change. By this time, embryos had developed into planulae competent to metamorphose (Plickert *et al.*, 1988). Metamorphosis was induced by ionic imbalance (Spindler and Muller, 1972; Weis and Buss, 1987). Competent planulae were transferred to a 53 m*M* CsCl solution in seawater. After approximately 4 h, planulae were placed on glass cover slips in seawater-filled six-well plates (1 planula per well). Attachment and metamorphosis occurred within 2 days. Six plates per cross (36 planulae total) were metamorphosed. Colonies were fed 3-day-old brine shrimp nauplii, followed by a complete water change each day.

Colonies were maintained in an incubator at 12.5°C for 50 days (to a mean size of 11 feeding polyps). The temperature conditions were chosen to reflect the ambient temperatures in Long Island Sound during the spring and early summer (Yund *et al.*, 1987). At this point in the seasonal cycle, sexual reproduction, recruitment, and intraspecific competition occur at high frequencies in this area (Buss and Yund, 1988). The duration of the experimental period was chosen for the purpose of assessing colony shape at small colony sizes. *Hydractinia* planulae display site-specific settlement on shells, hence the vast majority of intraspecific competitive encounters occur at small colony sizes (Yund *et al.*, 1987; Buss and Yund, 1988; Yund and Parker, 1989; see discussion below).

Using the protocols described above, colonies were measured for area and perimeter as soon as primary polyps and stolons developed after metamorphosis (<5 days). Each colony was measured at weekly intervals up to an age of 50 days (25–50% of the colonies of each cross failed to survive to this age). We analyzed the data using quantitative genetic techniques (Falconer, 1981). Because of the small size of the laboratory population, we suggest only very limited interpretation of our results with regard to the natural population of *Hydractinia*. Rather, we intended to gain further insight into the results suggested by the clonal repeatibility experiments; is shape largely genetically determined, *i.e.*, does shape variation have a large broad-sense heritability, and further, is there any evidence that the broad-sense heritability of shape variation in this laboratory population is due to narrow-sense heritability? Analyses were done on initial $perimeter/\sqrt{area}$ (age <5 days), on mean $perimeter/\sqrt{area}$ (for each colony, all shape measures up to age 50 days were averaged, and this mean value was used as the outcome), and on final $perimeter/\sqrt{area}$ (age = 50 days). These three comparisons correspond to before, during, and after stolonal mat formation.

Although our goals were somewhat different from typical quantitative genetic studies (*cf.*, Falconer, 1981), we used standard methods to examine the covariance of full sibs and the covariance of half sibs. Specifically, the between-female parent component of variance (i.e., $\sigma_{females}^2$, the variance between the means of the half-sib families) estimates COV_{HS} and measures additive genetic variance (*i.e.*, narrow-sense heritability, provided maternal effects are slight). The between-male parent component of variance, σ_{males}^2, estimates $COV_{FS} - COV_{HS}$ and measures a combination of additive and non-additive genetic variance (*i.e.*, broad-sense heritability, provided environmental effects are slight). Insight into additive and non-additive genetic variance can thus be obtained from a nested analysis of variance. The F-ratio of the male-parent mean square to the within-brood mean square will measure additive and non-additive genetic variance, while the F-ratio of the female-parent mean square to the male-parent mean square will measure additive genetic variance (see results below). We focus on qualitative interpretations of the analysis of variance rather than exact calculations of heritabilities because of the small size of the laboratory population and the limited goals of our breeding study (see Mitchell-Olds, 1986; Via, 1988).

To properly gauge the inheritance of shape, we attempted to reduce environmental effects in several ways. First, because we expected *a priori* that non-additive genetic variance would be large relative to additive genetic variance (*i.e.*, $COV_{FS} \gg COV_{HS}$, see discussion below), each female parent was mated to two male parents. Thus, any maternal or cytoplasmic effects (see discussion in Mazer, 1987) will inflate the covariance of the half sibs and inflate our estimate of additive genetic variance. Second, because matings were initiated at slightly different times and because between-mating environmental variation could inflate the covariance of the full sibs, environmental conditions were closely controlled. In addition to incubation at a constant temperature, seawater chemistry was monitored weekly, and nitrates and nitrites were maintained at low levels (≤9.0 ppm and ≤0.01 ppm, respectively). Salinity was maintained at ≈26 ppt. Any

variation in environmental conditions was slight and showed no systematic trend over the time course of the experiment. Finally, colony position effects were assessed. Stacks of culture plates (6 per mating) were kept on a single shelf in an incubator and positions were varied daily in a random manner. Individual plates, however, were kept in descending order (1–6), and culture wells were also in fixed positions. Because there was only one colony per well, wells were pooled into left wells, center wells, and right wells based on their positions in the six-well plate. The complete analysis was thus well position nested within plate, plate nested within male parent, and male parent nested within female parent. This analysis was carried out for intial and average shape measures. By the age of 50 days, the 25–50% mortality for each cross rendered the analysis of well position effects and plate effects unreliable because of missing values, and the pooled within-broods mean square was used as the error variance.

Further insight into environmental effects was gained by two additional experiments. First, for one of the maternal half-sib families, three 50-day-old offspring from each paternal cross were explanted onto snail shells occupied by hermit crabs and cultured in the 40-liter aquaria until each colony covered its shell and was fully mature. The 6 colonies were then compared using the method of clonal repeatibility described above, *i.e.,* 5 explants from each colony were grown on cover slips in a floating rack at 16°C and *perimeter/*$\sqrt{area}$ was measured at 10 days after explanting. These shape measures were then compared to the measures made on the colonies in their first 50 days of growth. Second, two colonies from each of three crosses were grown in the six-well plates as described above until they grew to the edge of the coverslip (60–120 days). Measures of *perimeter/*$\sqrt{area}$ were made at roughly weekly intervals.

Results

Growth morphology and shape

For the 242 50-day-old *Hydractinia* colonies measured, indices of peripheral stolon development (total colony perimeter/stolonal mat perimeter and total colony area/stolonal mat area) correlate highly with total colony perimeter divided by the square root of total colony area (r_s = 0.95 and 0.91, respectively). Because the correlated variables contain similar measures of total colony size (total perimeter, total area, or the square root of total area), the possibility of autocorrelation exists. For two reasons, however, the underlying structure of the data suggests that autocorrelation has negligible effects.

First, adjusting the correlated ratios to remove similar variables from each does not alter the correlations. Stolonal mat perimeter is highly correlated with the square root of total colony area (r_s = 0.94; note that r_s is insensitive to transformations of the correlated variables so that the correlation of stolonal mat perimeter and total colony area is also 0.94). Additionally, total colony perimeter is highly correlated with the ratio (total colony area)$^{3/2}$/stolonal mat area (r_s = 0.92).

Second, either measure of stolonal mat size (perimeter or area) shows a high correlation with total colony area (r_s = 0.94 and 0.92, respectively) but much weaker correlations with total colony perimeter (r_s = 0.63 and 0.53, respectively). Stolonal mat size is thus indicative of total colony area, but less so of total colony perimeter. These results are consistent with the stolonal mat showing circular growth in these small colonies, and deviations from circular growth being caused by peripheral stolons.

Shape variation in Podocoryne *and* Hydractinia

Measures of *perimeter/*$\sqrt{area}$ for both 7 and 14 days after explanting show that *Hydractinia* has more circular shapes than *Podocoryne* (Table I). To analyze these data, a natural logarithmic transformation was done to better meet the assumptions of the analysis of variance. The log-transformed data were first analyzed to assess the effects of the positions of the colonies within the racks, *i.e.,* replicates nested within species nested within positions nested within racks. Because of the different numbers of replicates

Table I

Shape variation in 15 strains of Podocoryne *and* Hydractinia[a]

	Podocoryne			*Hydractinia*		
Strain[b]	n	Age 7	Age 14	n	Age 7	Age 14
1	3	17.87 1.03	21.44 0.99	5	9.03 0.58	17.46 0.70
2	5	13.67 3.96	17.06 3.62	5	4.17 0.10	5.40 0.43
3	3	7.20 2.08	15.70 3.52	3	3.83 0.08	3.94 0.08
4	5	18.54 1.87	25.38 1.94	5	5.12 0.68	5.44 1.06
5	2	15.24 1.67	26.26 0.86	5	4.33 0.10	4.05 0.13
6	4	23.78 1.92	23.97 1.89	5	7.23 0.89	15.46 2.70
7	3	20.35 1.40	33.43 2.09	4	4.44 0.33	5.18 0.67
8	5	19.06 3.46	30.62 1.10	5	9.92 2.48	15.12 2.33
9	5	20.72 1.79	20.16 0.96	4	4.52 0.23	6.55 0.87
10	4	22.04 2.49	26.50 1.85	4	6.56 0.52	11.72 0.47
11	5	22.59 1.25	23.22 2.55	2	8.14 3.47	10.53 5.24
12	4	13.23 2.08	21.39 2.81	5	5.63 0.52	10.46 1.48
13	5	21.54 0.83	22.63 1.33	5	7.45 0.74	10.72 1.22
14	5	17.87 1.69	21.72 3.30	4	10.92 1.71	15.75 1.03
15	4	10.63 2.43	19.15 0.73	5	11.07 1.31	19.81 1.06

[a] Shape measures are *perimeter/*$\sqrt{area}$; means and standard errors are shown for n replicates of each strain, 7 and 14 days after explanting.

[b] For *Podocoryne,* strains 3, 7, 9, 13, and 15 are females, and for strain 3 at age 14 n = 2. For *Hydractinia,* strains 3, 5, 12, 14, and 15 are females, and for strain 14 at age 14 n = 3.

(some replicates were lost due to mortality, see Table I), the nested ANOVAs were unbalanced, although examination of the coefficients of the variance components indicated a high reliability of the F-tests carried out (see discussion in Sokal and Rohlf, 1981). At day 7, there is a strong effect of species ($F = 26.95$, d.f. = 15, 98, $P \ll 0.001$), but no effect of position ($F = 0.06$, d.f. = 12, 15, $P > 0.99$) or rack ($F = 1.05$, d.f. = 2, 12, $P > 0.35$). Similarly, at day 14, species shows a strong effect ($F = 26.96$, d.f. = 15, 96, $P \ll 0.001$), while position ($F = 0.19$, d.f. = 12, 15, $P > 0.99$) and rack ($F = 0.70$, d.f. = 2, 12, $P > 0.50$) do not. Based on this analysis, position effects were dropped from the model; this allowed including the strain effects (*i.e.*, replicates within strains within species within racks, see Table II). Again, because of the different numbers of replicates, this ANOVA is also unbalanced. Examination of the coefficients of the variance components (Table II) suggests that F-ratios should be reliable; in particular, the F-ratio assessing the effects of racks (i.e., $MS_{racks}/MS_{species}$) is highly reliable, while the F-ratio assessing the effects of species (*i.e.*, $MS_{species}/MS_{strains}$) is slightly conservative. The results are similar to the first analysis; there is no effect of racks ($F = 0.02$, d.f. = 2, 3, $P > 0.95$) and a strong effect of species ($F = 20.45$, d.f. = 3, 24, $P \ll 0.001$). Further, strains within species show significant variation ($F = 4.99$, d.f. = 24, 98, $P \ll 0.001$). Results at 14 days are similar; racks show no effect ($F = 0.03$, d.f. = 2, 3, $P > 0.95$), while species ($F = 12.94$, d.f. = 3, 24, $P \ll 0.001$) and strains ($F = 8.11$, d.f. = 24, 96, $P \ll 0.001$) show strong effects.

In addition to shape differences, *Podocoryne* exhibits faster growth rates than *Hydractinia* (Table III). Specific growth rates of polyps show no effect of racks ($F = 0.21$, d.f. = 2, 3, $P > 0.80$), but significant effects of species ($F = 11.75$, d.f. = 3, 24, $P \ll 0.001$) and of strains ($F = 3.79$, d.f. = 24, 96, $P \ll 0.001$). Similarly, specific growth rates of colony areas show no effect of racks ($F = 0.35$, d.f. = 2, 3, $P > 0.70$), a moderate effect of species ($F = 6.70$, d.f. = 3, 24, $P < 0.01$) and a strong effect of strains ($F = 2.90$, d.f. = 24, 96, $P \ll 0.001$).

Table II

Analysis of variance table for log-transformed shape measures at day 7 of the clonal repeatibility experiment

Source	d.f.	Mean square	Composition of mean square
Between racks	2	0.104	$\sigma_{error}^2 + 4.00\sigma_{strain}^2 + 20.00\sigma_{species}^2 + 40.00\sigma_{rack}^2$
Between species within racks	3	10.897	$\sigma_{error}^2 + 4.02\sigma_{strain}^2 + 20.08\sigma_{species}^2$
Between strains within species	24	0.497	$\sigma_{error}^2 + 4.22\sigma_{strain}^2$
Between replicates	98	0.099	σ_{error}^2

Table III

Specific growth rates for 15 strains of Podocoryne *and* Hydractinia[a]

	Podocoryne			*Hydractinia*		
Strain	n	Area	Polyp	n	Area	Polyp
1	3	0.211 0.01	0.197 0.01	5	0.181 0.01	0.184 0.01
2	5	0.181 0.05	0.169 0.02	5	0.034 0.01	0.00 0.00
3	2	0.110 0.09	0.071 0.07	3	0.059 0.06	0.013 0.04
4	5	0.226 0.01	0.166 0.02	5	0.038 0.01	0.035 0.02
5	2	0.130 0.06	0.069 0.04	5	0.102 0.01	0.113 0.02
6	4	0.195 0.01	0.138 0.02	5	0.092 0.03	0.074 0.03
7	3	0.203 0.01	0.170 0.03	4	0.124 0.01	0.123 0.01
8	5	0.220 0.01	0.197 0.01	5	0.176 0.02	0.101 0.02
9	5	0.184 0.03	0.171 0.02	4	0.063 0.01	0.071 0.03
10	4	0.174 0.02	0.166 0.03	4	0.113 0.03	0.100 0.02
11	5	0.191 0.01	0.215 0.01	2	0.050 0.03	0.019 0.08
12	4	0.101 0.06	0.220 0.03	5	0.100 0.01	0.079 0.01
13	5	0.192 0.02	0.207 0.01	5	0.102 0.01	0.148 0.02
14	5	0.112 0.03	0.181 0.02	3	0.144 0.01	0.042 0.03
15	4	0.158 0.03	0.137 0.02	5	0.192 0.01	0.079 0.02

[a] Specific growth rates (1/day) for total colony area and polyp number for 7 to 14 days after explanting; strains are designated by the same numbers as in Table I, and means and standard errors are shown for n replicates of each strain.

Breeding studies

For the breeding experiments conducted with *Hydractinia*, the shapes of the colonies initially and at 50 days (Table IV) show little correlation ($r_s = -0.06$, $P > 0.30$, for all 242 50-day-old colonies). This likely results from growth changes associated with stolonal mat formation (Fig. 1). Despite such variation, analyses of initial, average, and final colony shape all suggest a highly significant effect of the male parent and a non-significant effect of the female parent. For initial colony shape, there is no effect of the female parent ($F = 0.98$, d.f. = 4, 5, $P > 0.45$), a strong effect of the male parent ($F = 7.39$, d.f. = 5, 50, $P \ll 0.001$), and no effect of either plate ($F = 0.85$, d.f. = 50, 119, $P > 0.70$), or well position ($F = 0.95$, d.f. = 119, 173, $P > 0.60$). Similarly, for average colony shape there is no effect of the female parent ($F = 0.44$, d.f. = 4, 5, $P > 0.75$) and a strong effect of the male parent ($F = 15.21$, d.f. = 5, 50, $P \ll 0.001$). Again, there was no effect of either plate ($F = 0.88$, d.f. = 50, 119, $P > 0.65$) or well position ($F = 1.04$, d.f. = 119, 173, $P > 0.40$). For both initial and average shape analyses, the coefficients of the variance components (Table V) indicate a high reliability of the F-ratios. For final shape measures, missing values (because of mortality) rendered the analysis of position

Table IV

Descriptive statistics for the 10 crosses used in the breeding studies[a]

	Initial		Average		Final		
Parents[b]	n	Shape	n	Shape	n	Shape	Polyp
15 × 11	36	5.86 0.25	36	8.36 0.47	23	11.44 0.91	19.6 3.1
15 × 13	36	6.61 0.39	36	6.71 0.40	28	6.75 0.54	8.3 1.2
12 × 7	36	7.26 0.30	36	6.17 0.20	28	4.99 0.38	11.1 0.9
12 × 2	36	7.08 0.36	36	7.85 0.28	23	8.98 0.70	5.4 1.0
5 × 8	36	7.77 0.42	36	7.98 0.29	21	6.78 0.73	12.2 1.4
5 × 9	36	7.90 0.35	36	6.87 0.30	19	6.76 0.68	11.9 1.4
14 × 1	36	8.56 0.46	36	8.74 0.34	31	6.59 0.61	19.7 1.1
14 × 10	28	5.55 0.23	28	5.63 0.22	17	6.74 0.76	19.5 2.4
3 × 4	36	7.11 0.37	36	6.28 0.27	27	4.13 0.14	8.4 0.9
3 × 6	36	6.09 0.34	36	6.18 0.34	25	5.64 0.56	8.0 1.2

[a] Sample sizes (n), means and standard errors for shape measures ($perimeter/\sqrt{area}$) from initial colonies (primary polyps < 5 days old), average colonies (for each colony, all shape measures up to 50 days were averaged; this mean value was used for the descriptive statistics), and final colonies (50 days old). Data on polyp number (mean and standard error) is also presented for the final colonies.

[b] Numbers designating female parent and male parent respectively; the numbers correspond to the strains of *Hydractinia* from Tables I and III.

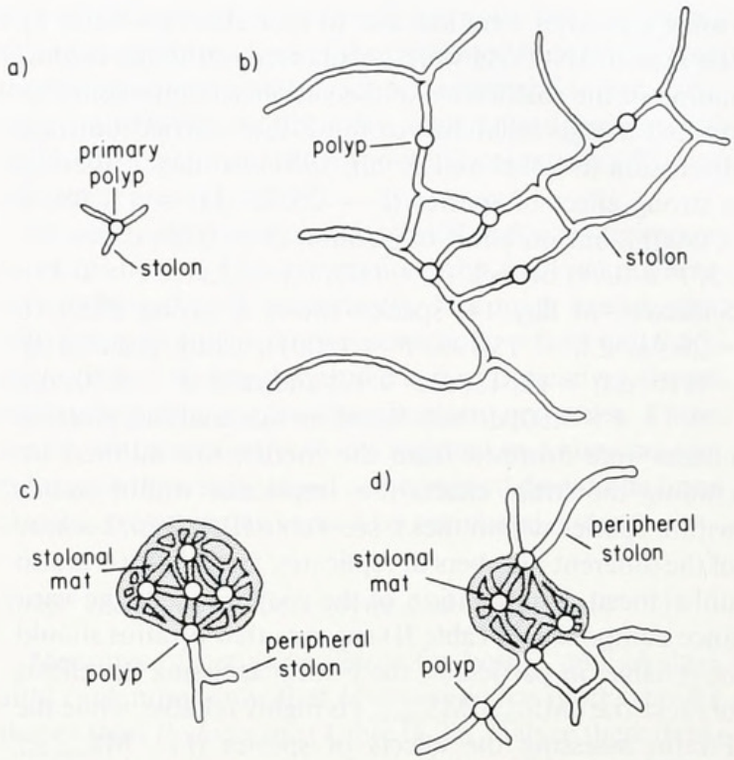

Figure 1. Rough schemata of (a) a primary polyp of a hydractiniid hydroid, (b) a small *Podocoryne* colony, and small *Hydractinia* colonies of the (c) "mat type," with few peripheral stolons, and the (d) "net type," with more peripheral stolons. Colonies are drawn as if encrusting the surface of the page; polyps would project up out of the plane of the paper. In the stolonal mat (the central portion of the *Hydractinia* colonies represented by the stipled pattern), the spaces between the stolons are filled with tissue; thus these stolons are fused together, while the peripheral stolons outside the stipled area (and those in *Podocoryne*) are unfused. Colonies are drawn to roughly the same scale; stolon width is approximately 70 microns.

effects unreliable; nevertheless, using the pooled within-broods mean square as the error variance, the data suggest a non-significant effect of the female parent (F = 1.23, d.f. = 4, 5, $P > 0.40$) and a large effect of the male parent (F = 11.3, d.f. = 5, 232, $P \ll 0.001$). Overall, the slight effect of the female parent (*i.e.*, a non-significant covariance of the half sibs) indicates that $\sigma_{females}^2$ is relatively small and that both maternal effects and additive genetic variance are correspondingly small. On the other hand, the large effect of the male parent suggests a large covariance of the full sibs, a relatively large σ_{males}^2, and likely a large non-additive genetic variance, given the closely controlled environmental conditions. The interpretation of these results should be limited to the small laboratory population on which the breeding studies were based (see Discussion).

While environmental effects could not be tested directly with this experimental design, the six offspring raised on hermit crab shells and then compared using clonal repeatibility allow an assessment of the sensitivity of *Hydractinia* colony morphology to environmental circumstances. These colonies were from crosses 15 × 11 and 15 × 13 (see Table IV); Figure 3 shows the shape measures for the 50-day ontogenies of the young colonies. After these young colonies were grown to maturity on hermit crab shells, explants were made; Figure 3 also shows the mean shape measures for five 10-day-old replicates from each of the mature colonies (means and standard errors for the 5 replicates of each colony are adjacent to the symbol for the 50-day shape measure for that colony). Comparing these shape data generated by different methods suggests that, despite different culture conditions, both methods generate roughly similar data for the same col-

Table V

Analysis of variance table for the analysis of the natural logarithms of average shape measures for each colony

Source	d.f.	Mean square	Composition of mean square
Between female parent	4	0.395	$\sigma_{error}^2 + 1.93\sigma_{well}^2 + 5.77\sigma_{plate}^2 + 34.60\sigma_{males}^2 + 69.21\sigma_{females}^2$
Between male parent	5	0.890	$\sigma_{error}^2 + 1.94\sigma_{well}^2 + 5.78\sigma_{plate}^2 + 34.65\sigma_{males}^2$
Between plate	50	0.059	$\sigma_{error}^2 + 1.95\sigma_{well}^2 + 5.82\sigma_{plate}^2$
Between well position	119	0.066	$\sigma_{error}^2 + 1.96\sigma_{well}^2$
Within well position	173	0.064	σ_{error}^2

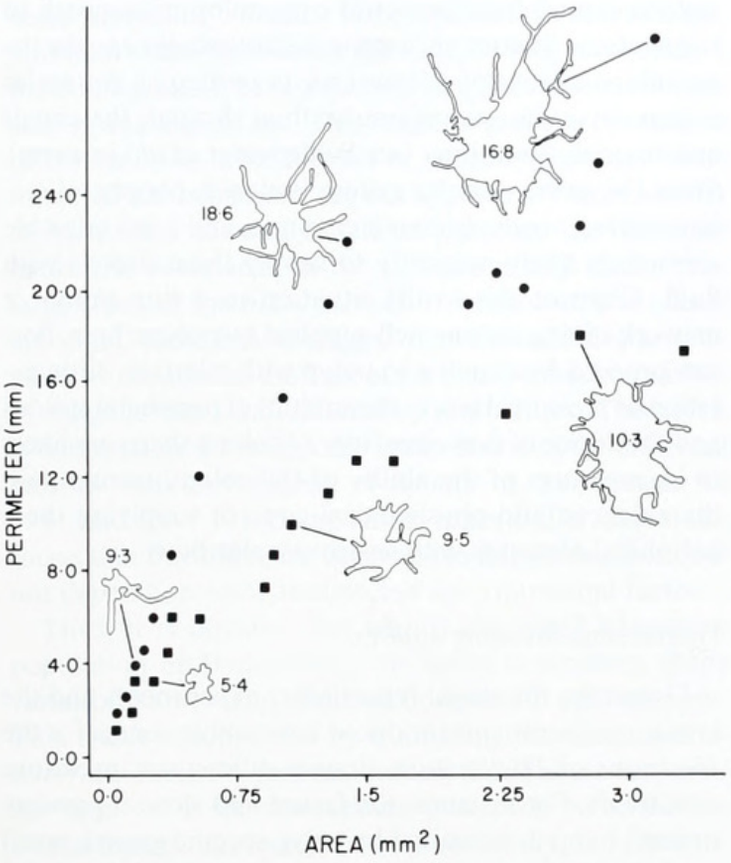

Figure 2. Perimeter versus area plots for two sibling *Hydractinia* colonies measured every other day for the first 5 weeks of ontogeny. Camera lucida tracings (not to scale) and shape measures (*perimeter/*$\sqrt{area}$) are shown for some of the data points. While shapes fluctuate as stolons branch and fuse, the two colonies exhibit distinct trajectories in perimeter versus area space.

ony, and, in particular, either method shows the differences between the crosses. At 50 days, cross 15 × 11 produced significantly more irregular shapes than cross 15 × 13 (Table IV); analysis of the clonal repeatibility data shows the same pattern. If the log-transformed shape data are analyzed as replicates nested within crosses nested within positions, there is an effect of cross ($F = 7.9$, d.f. = 3, 24, $P < 0.001$), but no effect of position ($F = 0.05$, d.f. = 2, 3, $P > 0.90$). Analyzing the data as replicates nested within strains nested within crosses provides a similar result (no significant effect of strains $F = 0.92$, d.f. = 4, 24, $P > 0.45$, but a significant effect of crosses $F = 22.7$, d.f. = 1, 4, $P < 0.01$). In either case, cross 15 × 11 exhibits significantly more irregular shapes than cross 15 × 13. This supports the findings of the breeding experiment and suggests that the differences between crosses are not the result of some undetected environmental factor varying over time.

The 6 colonies from 3 different crosses (12 × 7, 5 × 8, and 3 × 4 in Table IV) which were grown beyond 50 days (Fig. 4) show some variation in colony shape, but also suggest that differences among crosses are maintained at larger sizes. For instance, at 110 days, the 4 colonies which had not yet reached the edges of the cover slips suggest the same differences in shape, which were apparent for the complete crosses at 50 days (Table IV; for *perimeter/*$\sqrt{area}$, 5 × 8 > 12 × 7 > 3 × 4).

Discussion

These results have implications with regard to morphological variation in hydractiniid hydroids and in other clonal taxa as well. We discuss (1) the biological basis of shape in hydractiniid hydroids, (2) the implications of the *Hydractinia* breeding studies, (3) the general phenomenon of heterochrony in hydractiniid hydroids, and (4) the relevance of these results to other clonal taxa.

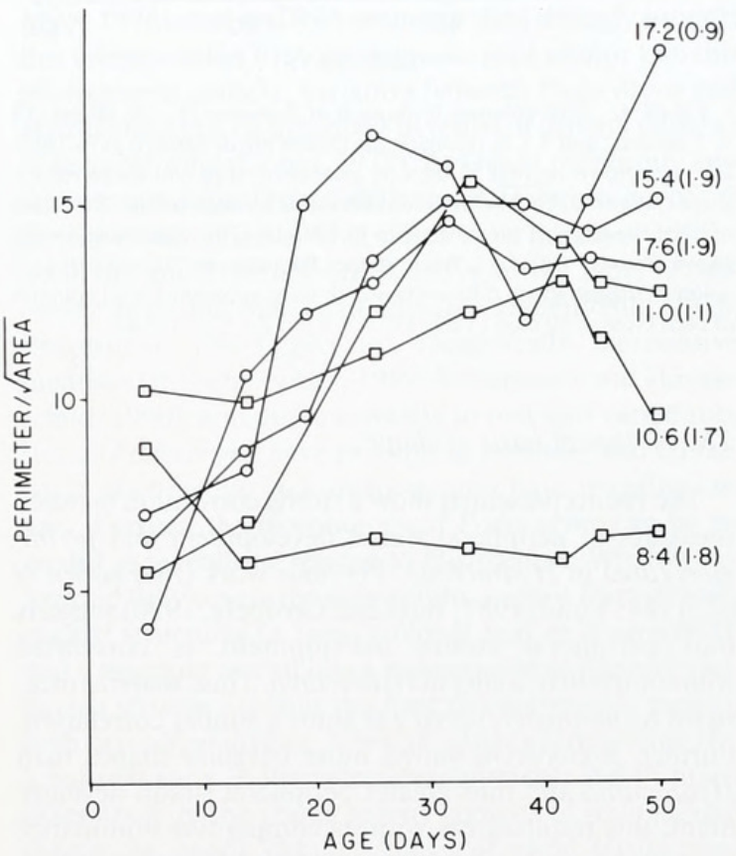

Figure 3. Shapes (*perimeter/*$\sqrt{area}$) of 6 colonies from one of the maternal half-sib families (3 from 15 × 11, shown by circles, 3 from 15 × 13, shown by squares; the crosses are designated as in Table IV) for the first 50 days of growth (lines connect points for each individual). These colonies were grown to maturity on hermit crab shells and then explanted and measured for shape again. Numbers adjacent to the symbol for the 50-day shape value show the means, with standard errors in parentheses, for 5 replicates of each colony 10 days after explanting. Despite differences in culture conditions, the clonal repeatibility shape measures and the shape measures for the first 50 days both suggest that colonies from 15 × 11 have more irregular shapes than those from 15 × 13.

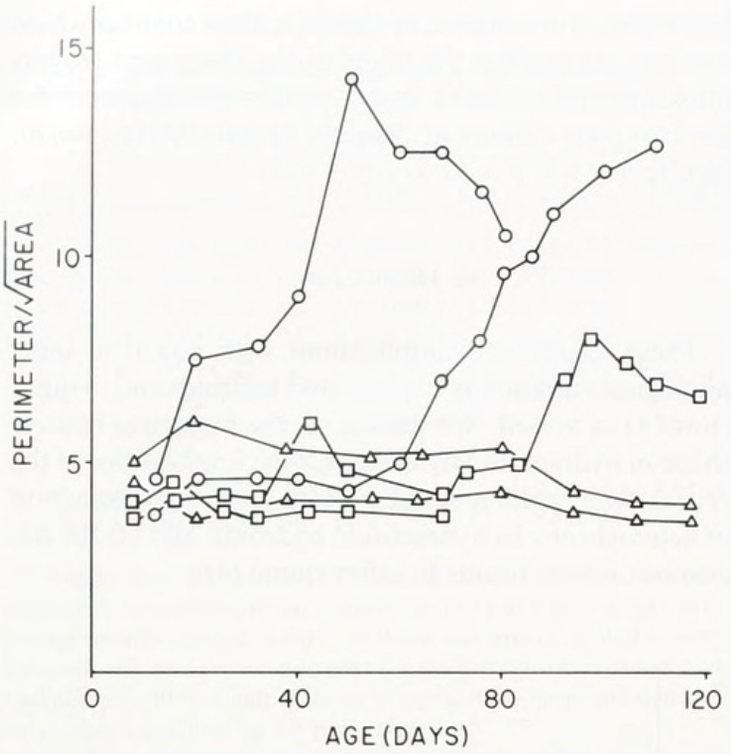

Figure 4. Two colonies from each of 3 crosses (5 × 8, circles; 12 × 7, squares; and 3 × 4, triangles; the crosses are designated as in Table IV) were grown beyond 50 days on glass cover slips and measured for shape (*perimeter/√area*). Lines connect values for each colony; 2 colonies reached the edges of the cover slips in <80 days; the remaining 4 were grown for over 100 days. While shapes fluctuate, at 110 days these 4 colonies suggest shape differences which were apparent for all colonies of each cross at 50 days (Table IV; 5 × 8 > 12 × 7 > 3 × 4).

The biological basis of shape

The results presented show a strong correlation between measures of peripheral stolon development and *perimeter/√area* in *Hydractinia.* Previous work (McFadden *et al.,* 1984; Yund, 1987; Buss and Grosberg, 1990) suggests that peripheral stolon development is correlated with competitive ability in *Hydractinia.* Thus, shape as measured by *perimeter/√area* will show a similar correlation. Further, *Podocoryne* shows more irregular shapes than *Hydractinia* and thus greater peripheral stolon development; this result agrees with its competitive dominance over *Hydractinia* in laboratory studies (McFadden, 1986). The correlations of shape with competitive ability can make measures of shape useful to biologists, but clearly shape differences are not causally related to competitive ability (see discussion below). Rather, shape, competitive ability, and peripheral stolon development are likely correlated consequences of the underlying dynamics of growth in these hydroids.

Shape measures bear a clearly interpretable relationship to these growth dynamics. Examining Figure 1 suggests that *perimeter/√area* will measure the degree to which stolons extend from a central ring stolon or network of ring stolons. Stolons encase the gastrovascular canals; the combined actions of stolons and, in particular, muscular polyps drive the gastrovascular fluid through the canals and nourish the colony (see Schierwater *et al.,* in press). Since the gastrovascular system is closed, peripheral stolons are essentially dead-end channels, and a considerable pressure is likely necessary to supply these stolons with fluid. Contrast this to the situation in a ring stolon or network of ring stolons well-supplied by polyps; here, flow can proceed from polyp to polyp with relatively little exertion of pressure. Hence, the amount of peripheral stolons and the degree of non-circularity of colony shape are likely to be measures of the ability of the colony to maintain the energetic and physiological costs of supplying these peripheral elements with gastrovascular flow.

Hydractinia *breeding studies*

Generally, the clonal repeatibility experiments and the breeding experiments produced compatible results for the 15 strains of *Hydractinia,* despite differences in culture conditions. For instance, the fastest and slowest growing strains (1 and 2, measured by polyp specific growth rates) produce the fastest and slowest growing offspring (14 × 1 and 12 × 2, measured by polyp number at 50 days), the strain with the most irregular shape (15) in one cross produced offspring with the most irregular shapes (15 × 11), and strains with nearly circular shapes (3 and 4) produced nearly circular offspring (3 × 4). The somewhat circular shape of colony 2 seems at variance with the irregular shapes of 12 × 2; however, this likely indicates the limitations of comparing developing colonies to clonal explants. Colony 2 shows extremely slow growth as do its offspring (12 × 2). It is likely that this slow growth reflects equally slow development of adult colony form and organization. The irregular shapes of young 12 × 2 colonies may indicate a slow transition from early colony development to adult morphology.

Despite the agreement of the results of the clonal repeatibility experiments and the breeding experiments, the latter can provide classes of information which are not available from the former. While only a small breeding study was carried out here, it is, to our knowledge, the first example of carefully controlled crosses for a clonal organism. To stimulate further such work, we will discuss the general value of such data. Clonal repeatibility studies demonstrate a significant broad-sense heritability of the shape variation (the strain-within-species effect in the ANOVAs). The breeding studies not only demonstrate a significant broad-sense heritability (the effect of the male parent in the ANOVAs), but also provide information on the sorts of genetic variation that constitute this broad-

sense heritability. For the three analyses (initial, average, and final shape measures), $MS_{females}/MS_{males}$ is roughly 1 (0.98, 0.44, and 1.23 respectively, see Results) and in each case is non-significant. This suggests that the covariance of the half-sibs is small, that is, progeny from the same maternal half-sib family are not appreciably more similar to each other than to unrelated progeny. On the other hand, the covariance of the full-sibs is high (hence the large effect of the male parent). If environmental effects are slight, these results suggest that non-additive genetic variance constitutes the bulk of the broad-sense heritability of shape in this small laboratory population. This result is bolstered by the additional study of one of the maternal half-sib families (progeny of female 15, *i.e.*, crosses 15 $\times$ 11 and 15 $\times$ 13). Using clonal repeatibility, this study shows that the difference between the full-sib families does not depend on some undetected environmental factor.

Thus, it is possible that within this small laboratory population of *Hydractinia*, the genes controlling shape variation show high levels of dominance and epistasis. This result is supported by examining the data qualitatively. In Table IV, paternal full-sib families are very similar (*e.g.*, note the low standard errors). Nevertheless, within a particular maternal half-sib family, full-sib families are often very different (*e.g.*, progeny of females 3, 12, and 15). Thus, the expression of the shape phenotype seems to depend on the interactions between the maternal and paternal genes (*i.e.*, dominance and epistasis). This result is intriguing in view of what is known about the ecology of this species. An increasing body of evidence suggests that competition for space has resulted in selection on growth morphology in *Hydractinia* species. Briefly, when two or more colonies of the same size encrust the same substratum, the colony with the greater peripheral stolon development will predominate (Buss *et al.*, 1984; Yund *et al.*, 1987; Buss and Grosberg, 1990), because peripheral stolons are capable of differentiating into a specialized aggressive organ, the hyperplastic stolon (Buss *et al.*, 1984; Lange *et al.*, 1989). Further, such competition is common in nature (Buss and Yund, 1988; Yund and Parker, 1989), and geographic variation in growth morphology correlates with the frequency of competition (Yund, 1987). Nevertheless, while this evidence suggests that natural selection favors colonies with extensive peripheral stolon development, colonies with little peripheral stolon development are present in the population of *Hydractinia symbiolongicarpus* sampled (see shape measures in Table I, and see McFadden *et al.*, 1984) and in other *Hydractinia* populations (Yund, 1987).

The results of the breeding experiment indicate a possible explanation for the maintenance of morphological variation in *Hydractinia* populations. While limits to the effects of natural selection are usually caused by countervailing selection, rather than exhaustion of additive genetic variance (see Lande, 1988), the latter has been implicated in a number of studies (*e.g.*, see Falconer, 1981; Lynch and Sulzbach, 1984; Hilbish and Koehn, 1985; Berven, 1987; Travis *et al.*, 1987; Emerson *et al.*, 1988; Gibbs, 1988). Possibly, this has occurred in *Hydractinia* populations, *i.e.*, natural selection has removed much of the additive genetic variation controlling peripheral stolon development, and what remains may be largely non-additive (*i.e.*, subject to epistatic and dominance effects) and thus masked from selection. We suggest this only as a possibility for directing future work; the small size of the laboratory population of *Hydractinia* precludes any firm generalization to natural populations.

Heterochrony in hydractiniid hydroids

Using morphological criteria, *Podocoryne* and *Hydractinia* have been grouped in the same family (*e.g.*, Mills, 1976), and mtDNA sequence data strongly support this interpretation (C. Cunningham, pers. comm.). In this phylogenetic context, variation between *Podocoryne* and *Hydractinia* can be described in terms of general patterns of heterochrony (Gould, 1977). As Gould points out, certain morphological traits often correlate with suites of life history characteristics. This seems to be the case with *Podocoryne* and *Hydractinia*. Relative to the latter, *Podocoryne* grow and mature rapidly (see Hauenschild, 1956; Braverman, 1963), produce energetically inexpensive medusae (*cf.*, Schierwater, 1989; Schierwater and Hauenschild, 1990), and disperse widely to new and varied substrata (*Podocoryne* have swimming medusae and larvae, while *Hydractinia* lack medusae and have crawling larvae). Further, the morphology of *Podocoryne* can be regarded as juvenilized relative to *Hydractinia*. When either hydroid fully covers the substratum, stolons form densely packed structures (a fused stolonal mat in *Hydractinia*, and a structure resembling a stolonal mat in *Podocoryne*). Such a structure is thus the final developmental stage in both taxa. *Hydractinia*, however, always forms some stolonal mat early in its colony development, and in many cases much of the young colony consists of stolonal mat (hence the nearly circular shapes of some *Hydractinia* strains). Very young (and sexually immature) *Hydractinia* thus attain a developmental stage (*i.e.*, fused stolonal mat and nearly circular shape) that is only approached by fully mature *Podocoryne*. The latter can thus be regarded as paedomorphic or the former peramorphic (see Alberch *et al.*, 1979).

Shape variation in clonal organisms

Many clonal plants, fungi, and invertebrate animals are composed of clonally iterated food-gathering units (*i.e.*,

ramets) connected by vascular canals (*e.g.*, stolons or rhizomes) that adhere to the substratum (Boardman *et al.*, 1973; Larwood and Rosen, 1979; Jackson *et al.*, 1985; Harper *et al.*, 1986). Clonal morphologies of this sort vary markedly in the development of peripheral stolons or rhizomes (Buss, 1979; Jackson, 1979; Lovett-Doust, 1981; Harper, 1985). The approach used here to measure variation in peripheral stolon development in hydractiniid hydroids may prove useful in other analyses of clonal form. Simple shape measures such as $perimeter/\sqrt{area}$ can easily be acquired from properly lighted specimens with a simple pixel gradient detector (provided by most commercially available image analysis software). Use of such characters may have considerable technical advantages for the analysis of ontogenetic and phylogenetic changes in colony form.

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