Retrospect on Modular Organisms

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Modularity is a new term, but some associated ideas have been with us for a long time. Animals like bryozoans, traditionally recognized as colonial, would all be considered modular at this meeting. It has also been realized for a long time that reproduction can be asexual and produce individuals that differ only from developmental asynchrony or environmental effects. The concept of metamerism is likewise a venerable one, and involves the repetitive units of construction (Hardwick) or products of iterative growth (Mackie) characteristic of modularity.

Despite the antiquity of many of the concepts, I think it clear that there is something new about the idea of a modular organism. It is an idea that can give a benthic ecologist working on sea anemones a feeling that in some ways he may have more in common with a plant ecologist studying herbaceous perennials than with another benthic ecologist mainly interested in molluscs. It would appear that some participants at the meeting find cloning an unnecessary criterion, or metamerism an insufficient criterion of modularity.

What do we really mean by a modular organism?

It would be premature and obstructive for me to attempt a list of formal criteria for modularity and to insist that it be strictly applied. Everyone at the meeting would agree that strawberry plants are modular and that mammals and roundworms are not. There might not be much unanimity of opinion on a conceptual basis for such inclusion and exclusion. I will briefly discuss this possibly contentious issue mainly because the organizers neglected (or wisely avoided?) its inclusion in the formal schedule.

Its vegetative cloning process makes the strawberry so clearly modular. Most herbaceous annuals would be considered unitary (non-modular) organisms. They grow and mature where they germinate, bloom, produce genetically diverse seeds, and then die. A strawberry plant can do all these things and more. It can live beyond its first blooming, and it can send out one or more horizontal stolons, stems specialized for asexual reproduction. A stolon can continue its growth indefinitely, producing new plants at about half-metre intervals. Each new plant may also be able to send out additional stolons, so that the vegetative spread is a branching process, like that modelled in figure 2 of Bell (this symposium). It is this iteration of complex multicellular units, each capable of physiological and ecological independence by a branching growth process, that makes the strawberry modular.

In applying the modularity concept to other organisms, questions arise as to what in the strawberry life history is necessary or sufficient. Many of the organisms discussed at this meeting seem quite dissimilar to strawberries in many of the features listed. Is a physically demonstrable branching necessary? Even in the strawberry the stolons degenerate in a few months and no longer serve to connect members of the same clone. No one would insist that there be permanent

physical branches, but can the branching be purely conceptual, as in a pedigree diagram for a motile organism that reproduces by fission or budding? Can the buds be internally produced parthenogenetic eggs of maternal genotype? I would opt for including ameiotic parthenogenetic lineages among the modular, but think that at least a conceptual branching process is required. A merely linear repetition of parts like the segments of an earthworm would not suffice. So I would accept all of the models of modularity presented by Hallé except the Chamberlain model, which I would reject as merely metameric, not modular.

If an ameiotic parthenogenetic lineage is accepted as modular, what about a hybridogenetic fish like some forms of *Poeciliopsis* (Vrijenhoek 1984; p. 401)? A haploid set of chromosomes forms a genetic module that is replicated indefinitely, even through each member of the all-female hemiclone carries and expresses paternal genes that are disposed of at meiosis. Each individual is genetically unique, and littermates resemble each other only as much as full sisters normally do, but there is no recombination, and each individual is just as similar genetically to a remote ancestor or descendant as to a sister.

Modules can show different kinds and degrees of independence. The early rudiment of a strawberry plant on a stolon depends on its parent for water and nutrients. Only gradually does it take over the job of providing for itself. Each plant may also form another kind of reproductively specialized branch, one that ends in a flower. A flower depends for its upkeep on the plant that made it, but flowers are structurally similar units. This example shows that the criteria of modularity may depend on the interests of the observer. Even without vegetative cloning, a plant with more than one flower might be modular to a morphologist, or to an ecologist interested mainly in the functioning of flowers. To an ecologist interested in demography or trophic structures, only a cloning species would be modular.

It may prove useful to restrict the term modular organism to those that reproduce asexually, but to recognize that there are modular aspects of development and morphology in most unitary organisms. Apple trees are normally unitary, but apple blossoms are structural modules produced abundantly by each mature tree. Hair follicles and sweat glands on a mammal are structurally similar parts with some degree of functional independence, and they are produced by a cell pedigree that can be represented as a branching process. The gametogenesis of any organism depends on a branching pedigree of meristem or germ-line cells that produce functionally similar and independent gametes.

CAUSES, CONSEQUENCES AND MACROEVOLUTION OF MODULARITY

Modularity has been regarded as a solution to problems of size and scaling. Up to a point, material invested in the corolla of an apple blossom is more than compensated by expected reproductive payoff. Beyond that point the odds are less favourable, and fitness is better served by making flowers more numerous, rather than larger. Likewise the nutrients captured by a hydra are best invested in growth, up to a point, beyond which investment in a bud is more profitable. A clone of a hundred may have the same ratio of surface to volume as a single hydra. A hydra of a hundred times the mass of a normal one would have only about one fifth as much surface per unit mass. This means only one fifth of the gut surface for absorbing nutrients, and one fifth of external skin for respiratory and excretory exchanges. I doubt that such a hydra could meet its maintenance requirements in even the best of environments.

This kind of thinking can be overdone, and it is important to realize that there are many

ways of coping with increasing size, in both ontogeny and phylogeny. If one assumes that increasing maintenance requirements for an increasing mass of tissue will eventually consume all available resources, with none left for growth or reproduction, it is easy to show that it is adaptive for growth to stop short of the maximum attainable size. Sebens (1982) thus modelled the optimum size at maturity for a sea anemone. Such modelling ought to be widely applicable, for instance, to the growth and maturation of a fish like the guppy, as it grows from about 5 mm to several centimetres. If an increasing maintenance burden causes guppies to curtail growth and start reproducing at a few centimetres what about a bluefin tuna? It starts its independent existence considerably smaller than a newborn guppy, and may end it at about a hundred thousand times the mass of an adult guppy. Are we to suppose that a milligram of larval and a milligram of adult liver tissue must have the same maintenance cost?

Ryland and Warner seem to accept Sebens' line of reasoning, although they review a diversity of measurements of uptake efficiencies and maintenance costs in relation to size in a variety of organisms. Most indeed support the idea that potential for resource capture may fail to keep pace with metabolic costs as an organism grows, but the data are so variable as to be compatible with a variety of conclusions. Also some deficiencies pervade the cited studies. Very few investigate even as much as a ten-fold mass difference between the largest and smallest specimens. Some unitary organisms (indeed, some modules, such as aspen trees) grow many orders of magnitude during development, often without obvious allometric changes. A 1 cm tuna and a 1 m tuna have much the same shape and life style.

Another problem is the inclusion of both mature and juvenile specimens in the same study. If a guppy's growth rate is less between 3 and 4 cm than it was between 2 and 3 cm, I would be inclined to attribute it to a shifting of resources from growth to preparations for reproduction, not an adjustment to a changing surface : volume ratio.

If one forgets about maintenance costs and assumes that an organism grows at a rate simply determined by surface area and does not change shape as it grows, its rate of length increase will be constant with time, and its mass proportional to the cube of time. The approximate accuracy of this simple formulation is indicated by the lack of any strong dependence of growth rate on absolute size in fishes. Both juvenile sharks 2 m long and larval fishes a few millimetres long commonly grow about 0.3 mm per day (Taylor & Williams 1984).

My reservations relate only to a facile use of surface : volume considerations in explaining module size, not from any doubt on the importance of scaling effects in evolution and ontogeny. I see no alternative to the use of size-optimization models in explaining the similarity of flowers on a tree, or peas in a pod, or zooids in a benthic colony. My inclination would be to explain size uniformities on the basis of ecological specialization, for special prey species of a sea anemone, or preferred pollen vectors for a flowering plant.

Whatever the reason, the continued growth of a module, or even a phalanx of modules, will eventually produce a size at which further investment in growth will not be the optimum use of resources. A phalanx might escape from this bind by abandoning the phalanx for the guerrilla mode of proliferation. Another escape might be investment in widely dispersed propagules, perhaps sexually produced, that can start new phalanges elsewhere. Still another is to indulge in a higher level of modularity and build a phalanx of phalanges as shown by various corals (Rosen). Mackie and others at the meeting spoke of levels of modularity, with the most basic level that of the cell or even the organelle.

Still another solution to the problem, of maintaining optimal module or phalanx size, is

module specialization or even the abandonment of modularity. It is widely accepted that multicellularity in organisms more than a few millimetres in size depends on cell specialization. It is equally understandable that masses of multicellular modules may function better if modules in different regions specialize in various ways for the collective interest of the colony. A siphonophore is made up of what, to a morphologist, are modular elements. Yet in many aspects of its biology, as discussed in Mackie's chapter, a siphonophore is very much a unitary organism: its different parts shown extreme specialization, and a subordination to the interests of the entire unit; information is rapidly transmitted between widely separated regions; and most of the growth is from metameric rather than branching addition of parts. A parallel regression of modularity is shown by salps and by Palaeozoic graptolites, as shown by Bates & Kirk (1986).

Some degree of modularity is the general rule in the plant kingdom, is widespread in many animal phyla, and must have appeared independently in many lines of descent. Yet closely detailed convergences may be noted between phylogenetically remote groups, as several participants pointed out. Trinci and Cutter, for example, listed some remarkable similarities between prokaryote and eukaryote soil inhabitants. Only a small proportion of the topographically possible systems of modular proliferation, as explored in Bell's simulations, have actually been found in living organisms. No detailed explanations for such limits on evolved forms of modularity were advanced at the meeting, although there seemed a general agreement that many mathematically possible systems would be functionally maladaptive for any organism.

The absence of broad ranges of character complexes from the earth's biota shows that the evolutionary process is constrained. A major constraint is natural selection, which prevents the production of organisms of less than some minimum level of viability. To say that only some of the conceivable patterns of modularity would be viable is to invoke natural selection. The idea of evolutionary constraint is sometimes used in more than this sense. Holder (1983) proposed that the machinery of vertebrate development is incapable of producing more than a limited range of modification in tetrapod limb and digit patterns. I suggest that this may be analogous to a comparative anatomist of wheels concluding that manufacturing processes are unable to make wheels of other than nearly perfect circularity.

The logically possible forms of modularity may be compared to the forms of swimming animals. Here also there are some often cited examples of convergence, for instance on streamlining, and the repeated use of only three kinds of thrust: jet propulsion, paddling, and longitudinal undulation. Within each of these modes of movement only a small number of possibilities are repeatedly utilized. Sharks and crocodiles swim by horizontal undulations, whales and leeches by vertical ones. Nothing swims by undulations in any other plane. I suspect that we all feel that we understand these examples of evolutionary constraint. When we know as much about the functional and phylogenetic aspects of modularity as we do about swimming, the limitations may have equally obvious explanations.

I wonder whether it may be that today's forbidding constraint may turn out to be tomorrow's adaptive breakthrough. Biologists in the Ordovician no doubt would have proclaimed that only a rudimentary dry-land biota would ever be possible, in the Silurian that aerial flight could never be evolved, and so on. Rather than say that certain evolutionary developments are impossible, I would prefer to use Bell's phraseology, that there are ' ...forms yet to be realized '. Maybe the lands will someday be clothed in forests of the cross-braced trees that Hardwick says can't happen.

ECOLOGY AND MICROEVOLUTION OF MODULAR ORGANISMS

Ecological differences between unitary and modular organisms were emphasized by most of the speakers at the meeting. Many are listed in the first paragraph by Jackson and Coates. The differences really are important and their neglect surprising. There have been great advances in demographic theory, but almost none are applicable to the many species for which we need to count both genets and modules. A module-relevant demography based on size rather than age is only beginning to be developed (Hughes 1984; Taylor & Williams 1984). Such generalizations as those advanced by Jackson and Coates on range of larval dispersal in relation to presence or absence of cloning could only have been proposed by someone convinced that the presence or absence of cloning is an important difference.

Many studies of community ecology assume that sessile organisms disperse only in such early stages as larvae or seeds and thereafter can make no habitat selection. Thus they neglect the fact that some of the sessile forms may be modular and users of the guerrilla strategy. The distribution of some of the plants in a weedy field or invertebrates in a benthic community may be poorly related to the distribution of the seedlings or larval settlers from which they developed, perhaps years (or centuries) before. Jackson and Coates mention a stoloniferous invertebrate that may spread as much as 72 cm a year, and this may be much less than the rate of spread of some terrestrial plants (Harper 1985). This sort of clonal growth, followed by a disappearance of modules from regions not permanently suitable, must have a major effect on the ecological distribution of guerilla strategists.

Franco's observations, that trees can greatly modify their growth patterns in relation to immediate environmental conditions, suggest the additional possibility of an actively biased clonal proliferation in an environmental gradient. The avoidance reactions of soil hyphae discussed by Trinci and Cutter would lead to an active habitat selection, and a similar phenomenon was recently reported for a higher plant. Salzman (1985) showed that rhizomes of *Ambrosia psilostachya* in saline soils grow preferentially towards regions of lower salinity. This means deprivation and perhaps abandonment of members of the clone living in higher salinities. This sort of chemotropic growth of a clone differs from chemotactic habitat selection by a motile animal mainly in the time scale of events.

Modularity can have a major effect on the genetic structure of a population, a matter touched on briefly by Jackson and Coates but otherwise neglected at the meeting. The blossoms on an apple tree are reproductive modules, not much different in principle from the gonozooids on a hydrozoan colony. The great number of these modules on one tree must make it improbable that a bee visiting a flower has just come from another tree. Large apple trees must have greater difficulty than small ones in getting their pollen dispersed and their ovules fertilized by pollen nuclei from other trees. Likewise, a strawberry clone that succeeds in the dense occupation of a large area must get mainly within-clone pollen transfer. A clonally spreading plant must either be self-compatible and little affected by inbreeding depression, or have special mechanisms for increasing the likelihood of outcrossing. Some examples and general discussion are provided by Handel (1985).

Cloning raises the likelihood that associated conspecifics are genetically identical, and such association may be sufficiently predictive of genetic similarity to result in kin-selected altruism and cooperation. The colony integration discussed by Ryland and Warner and the more extreme subordination of originally independent zooids discussed by Mackie are attributable

to this factor. Long-term physical communication or contact may not be needed. A reliable sensory connection may suffice, as is shown by the sterile castes of parthenogenetic aphids (Aoki 1977).

The theoretical development of population genetics, like that of demography, was undertaken for unitary organisms. The mutation rates one reads about in the textbooks would inflict serious genetic loads on clones in much less time than they commonly persist. There is some evidence for this effect in parthenogenetic fishes (Vrijenhoek 1984) and it should be looked for in other forms in which a clonal life cycle passes through a single-cell stage. Where cloning is vegetative, mutations can perhaps be weeded out by the diplontic selection discussed by Hardwick. I hope it will not be too long before diplontic selection is discussed in the textbooks.

In the population genetics developed for unitary organisms, an age cohort is expected to be replaced within a few times the period of development from zygote to maturity, to remain close to Hardy–Weinberg equilibrium, and to show only minor changes in gene frequency. It is abundantly clear, from the few genetic studies that have been carried out, that modular organisms need not conform to such expectations. Clones of rapidly developing organisms with genotypic life spans measured in millenia were mentioned by a number of speakers. Gross departures from Hardy–Weinberg ratios have been observed in such diverse groups as sea anemones (Ayre 1984), *Daphnia* (Lynch 1983), and clover (Burdon 1980). It is also clear, as pointed out by others at the meeting, that variation in reproductive success among individual genotypes of modular organisms can be orders of magnitude greater than would be expected of unitary forms. I join Harper (1985) in wondering why '...so much of the study of ecology and evolution has been based on the behaviour of unitary organisms'.

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