
Preface

J. L. Harper, B. R. Rosen and J. White

Phil. Trans. R. Soc. Lond. B 1986 **313**, 3-5

doi: 10.1098/rstb.1986.0021

Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)

To subscribe to *Phil. Trans. R. Soc. Lond. B* go to: <http://rstb.royalsocietypublishing.org/subscriptions>

PREFACE

Contributors to this Discussion Meeting were given only the most general guidance to what is meant by ‘modular’. The letter of invitation said “By ‘modular’ we imply growth of the genetic individual by the repeated iteration of (multicellular) parts – modules. This means that we can consider together at the meeting the growth and form of corals, higher plants, fungi, . . ., ascidians, . . ., bryozoans, etc.”.

Modular growth contrasts with ‘unitary’ growth, in which the zygote develops to a determinate structure that is repeated only when a new life cycle is started from a single-celled stage, usually a zygote. Of course most unitary organisms bear repeated parts, such as legs, wings and body segments, but they are formed in early embryogenesis, not by continued or prolonged somatic iteration, and their numbers are usually very strictly determinate. We might count the numbers of flies in a population of *Drosophila* by counting the numbers of legs and dividing by six, or of birds by counting the wings and dividing by two. There is no such determinate divisor for the genetic individual (genet) of a modular organism – no determinate number of leaves or buds on a tree, polyps on a coral, hyphae in a fungal colony or branches on a root system. Modules themselves, however, may be quite strictly determinate in form, e.g. the number of petals on a flower, the number of leaflets on a leaf.

In many of the papers in this volume authors have attempted their own more precise definition of ‘module’, usually one especially appropriate for the class of organisms in which they are especially interested. Students of particular groups tend to search for homologies among structures and to define modules as homologues. When comparisons are made across the plant and animal kingdoms, it is analogies rather than homologies of structure that give unity to the concept of modular organisms. In this broader vision the module is the multicellular unit of structure that is iterated in the process of growth. There is no obvious homology between the polyp of a coral and the leaf with its axillary bud on a tree, but the analogy is clear. Both are repeated units of structure.

Most modular organisms are branched; even those palms that fail to branch above ground bear branched root systems and inflorescences. It is the pattern of branching or budding that gives most modular organisms their overall form. This is at its most dramatic in the stark winter outlines of deciduous trees, which are often quite distinctive of various species, though fearfully difficult to describe in words. There is the same difficulty in describing the form of corals; indeed, the most effective description may involve likening them to particular plants, e.g. *Pectinia lactuca*, *Pectinia paeonia*, *Acropora hyacinthus*, *Pavona cactus*; mythical monsters, e.g. *Hydra*, *Medusa*, *Gorgonia*; or to the organs of unitary organisms, e.g. *Diploria cerebriformis* (a ‘brain’ coral), *Echinopora mammiformis*, *Psammocora digitata*, *Cycloseris patelliformis*, *Heteropsammia cochlea*.

Growth forms that develop by branching or budding may iterate multicellular structures at a variety of levels. Most trees are composed of branches, branchlets and twigs, which in turn bear leaves with axillary buds. Repeated units of structure – modules – may be recognized at each of these levels so that the form of the organism comes from a hierarchy of different orders of repeating units. This is in essence the same sort of hierarchical modularity that an architect recognizes in the repeated form of apartment blocks, apartments within blocks, rooms in the apartments and modular furniture within the rooms.

We can recognize two broad categories of form among modular organisms: that in which the modules remain attached to each other, and that in which modules or groups of modules become separated – organisms that fall to pieces as they grow. In situations in which modules remain attached to each other the form of the whole organism may depend on the accumulation of dead modules from the past. Quite unlike any unitary organisms, a large part of the body of some modular organisms is the accumulated ‘necromass’ of dead modules. It is this feature that gives trees, corals and mosses their peculiar role in creating structure in a community: forests, coral reefs and peat bogs have a community architecture that is an accumulation of dead modules bearing a thin skin of active feeding modules (polyps or leaves). The fact that most modular organisms occupy fixed positions in space means that they give a continuity to the spatial structure of communities that mobile unitary organisms cannot do.

An organism that is fixed in position in its habitat depletes resources locally. It cannot escape from the resource depletion zones that it creates except by growing away from them. Competition between individuals will commonly occur where such organisms are close enough to enter into each other’s resource depletion zones. One effect is that different parts of a single genet may meet quite different environments – a neighbour on one side and none on the other, or a neighbour of one species on one side and a different species on the other. The fitness of a single genet is then simultaneously tested in a variety of environments. The progeny that it leaves may derive almost entirely from a single branch that grows into an open space or into the territory of a weaker neighbour. Modular organisms of this sort allow the interaction between individuals to be studied in a reductionist detail that is virtually impossible in motile (i.e. most unitary) organisms.

The life cycles of modular organisms that fall to pieces as they grow are exemplified by many freshwater plants, e.g. among species of *Lemna*, *Eichhornia*, *Salvinia*, and among animals by *Hydra* spp. and *Fungia* corals. Old dead modules are sloughed off and, in marked contrast with trees and most corals, the population of modules remains permanently young. In these cases modules are free to move passively in the water, escape from each other’s resource depletion zones, and even disperse from habitat in floods (or, in the case of *Lemna*, on birds’ feet). The opportunity for a single genet to colonize extensive areas is maximized in these situations; in Britain, the whole population of a modular organism, such as the aquatic *Stratiotes aloides*, may perhaps be represented by just one single genet. In terrestrial communities there is less opportunity for modules to separate and disperse, though the bulbils of species such as *Allium vineale* are shoot modules that are dispersed in a manner similar to seeds. More usually terrestrial plants that grow to form clones become fragmented by the decay of their interconnecting parts, but the modules become dispersed only to the extent by which they have *grown* into new territory. However even in these cases, clones may be broken by burrowing animals or by ploughing, and some of the most aggressive weeds of agriculture, such as *Elymus repens* and species of *Oxalis* and *Cyperus*, are stimulated to multiply by such damage.

It is easy to see that there are some environments in which the fitness of a genet will be enhanced if the development of its parts is highly integrated and correlated and others in which it is to the benefit of the organism to allow its parts to respond very locally and independently. In *Hydra* and *Lemna* the loss of continuity between modules is part of the programmed course of development; hormonal and nutritional interdependence is wholly sacrificed. At the other extreme the highly organized structure and behaviour of siphonophores is ensured by specialized signalling between the modules. The continuum of forms between these two

extremes represents the range of compromises between freedom of the individual modules and subservience to the organized genet that has obvious parallels in political systems. How far modular organisms are composed of physiologically independent parts or of correlated integrated wholes may have to be answered differently for different species and may represent compromise responses to conflicting selection pressures.

Overwhelmingly modular animals and plants occupy fixed positions in their habitats or are moved passively by water or other agents. They are therefore denied the opportunity to search for and chase after prey or to run away from predators, seek suitable habitats or escape from competitors. They cannot actively search out mates (there are of course some unitary animals that face the same constraints, such as mussels and barnacles). Almost all the activities that involve mobility in unitary organisms become the responsibility of form in modular organisms and form, in turn, is the consequence of the pattern of growth. If it is not possible to run away from prey, natural selection may well favour the evolution of passive defences such as spines. If it is impossible to search and capture resources, structures may be favoured that attract or intercept them. If it is impossible for individuals to move in search of mates, some other force may be favoured that will move gametes or microspores between potential parents (or outbreeding must be sacrificed).

One of the most important of the properties of unitary organisms, the segregation of the germ plasm, does not hold for modular organisms. Germ plasm is repeatedly regenerated as module gives way to daughter module during the process of growth. This means that, at least in theory, somatic mutation could be a significant force in the evolution of modular organisms. This suggestion may be a red herring but the possibility has to be faced.

A further important quality conferred by modular growth is that the Fisherian reproductive value of a genet may increase with age. Modular growth allows, at least in theory, an exponential increase in the rate at which progeny are produced. Under these conditions the evolution of senescence may be greatly delayed or perhaps not occur at all. Instead it appears that the phenomenon of senescence has become expressed at the level of the module rather than the genet. There is little evidence that the life of the genet in most modular organisms has a natural span; in many species it appears potentially immortal.

The proceedings of this meeting show that there is a great area of biological research, only beginning to be explored, in which botanists and zoologists find much in common. Widely held general models of evolutionary processes, based on the study of unitary organisms, may be seriously upset by increased knowledge of how modular organisms behave. It may be that the distinction between the biology of modular and unitary organisms is more profound than the classic distinction between animals and plants.

February 1986

J. L. HARPER
B. R. ROSEN
J. WHITE