Iterated Ontogenies Reiterated

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Paleobiology, Vol. 15, No. 1 (Winter, 1989), 67-73.

STEHLI, F. G., AND S. D. WEBB (eds.). 1985. The Great American Biotic Interchange. Plenum; New York.

STURM, H. 1978. Zur oekologie der andinen Paramoregion. Biogeographica 14. W. Junk; The Hague.

TROLL, C., AND W. LAUER (eds.). 1978. Geographical Relations Between the Southern Temperate Zone and the Tropical Mountains. Franz Steiner; Wiesbaden.

VAN DER HAMMEN, T. 1974. The Pleistocene changes of vegetation and climate in tropical South America. Journal of Biogeography 1:3–26.

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Paleobiology, 15(1), 1989, pp. 67–73

Review

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The Growth and Form of Modular Organisms. Proceedings of a Royal Society Discussion Meeting held on 27 and 28 June 1985. Organized and edited by J. L. Harper, F.R.S., B. R. Rosen, and J. White. The Royal Society; London. 1986. First published in *Philosophical Transactions of the Royal Society of London*, Series B, *313*:1–250.

Modular Organisms. Case Studies of Growth and Form. Papers relating to a discussion on growth and form in modular organisms. Preface by J. L. Harper, F.R.S. First published in *Proceedings of the Royal Society of London*, Series B, *228*:109–124.

The mystery of ontogeny lies in the predictable unfolding of complex, organized life cycles and structures from apparently much humbler zygotes. In attempting to understand the intricacies of ontogeny, morphologists of the 19th century found some hope in their architectural analyses of plants and what they called zoophytes (i.e., sponges, colonial cnidarians, ascidians, and bryozoans), for it could be seen that substantial aspects of morphological complexity could be explained in terms of ontogenetic repetition in space and time. It is only over the last two decades, however, that serious attempts have been made to build a physiological, structural, genetic, and demographic framework for comparing organisms whose life cycles and morphologies are produced by iterated ontogenies to those organisms with simpler ontogenies.

The development of this framework, and the exploration of the ecological and evolutionary consequences of life cycles composed of iterated ontogenies, can be traced through a series of symposia dating back to the publication of *Animal Colonies* in 1973. As the title implies, the fundamental difference between life cycles characterized by single versus repeated ontogenies was visualized in terms of the morphological and physiological distinction between solitary and colonial animals. The sponges, as usual, showed the inadequacies of vocabulary. Several of the contributors recognized that sponges were somehow more similar to bryozoans, hydrozoans, and ascidians than they were to barnacles and mussels, yet sponge morphology could not be conveniently cast into the solitary/colonial dichotomy.

The publication of *Biology and Systematics of Colonial Organisms* in 1979 did little to clarify the ambiguities that were raised by the contributors to *Animal Colonies.* Despite B. R. Rosen's probing and often metaphysical analysis of the various meanings of coloniality, only a few authors considered the morphological, ecological, and evolutionary implications of iterated ontogenies. In contrast, John Harper's *Population Biology of Plants* (1977) marked a crucial point in the analysis of life cycles composed of repeated ontogenies. Harper's monograph was in many ways a synthesis of an arcane and voluminous literature on plant

0094-8373/89/1501-0009/$1.00

morphology and morphogenesis into the view of a plant being a hierarchically structured metapopulation of iterated modules, some of which retain the potential throughout ontogeny to give rise to more modules.

This way of looking at plant architecture portrayed ontogeny as a nested set of modular demographies. To the extent that modular construction facilitated genotypic fragmentation (i.e., asexual multiplication or clonality), a new demographic framework for analyzing the structure of life cycles had to be developed, as well. Accordingly, Harper coined the terms "genet" (which previously referred to the coat of the civet cat) to include all modules derived from the same zygote (independent of their spatial and temporal relationships) and "ramet" to designate what a demographer would typically count as an individual, independent of its genotypic identity.

Whether a module coincided with a ramet was, and remains, a matter of considerable confusion. Morphologists generally don't care: a module could be an apical meristem, a root, a shoot, a flower, a branch, a leaf, a polyp, or a zooid depending on the level of architectural analysis. Demographers seem not to care either, for their fundamental concern is with counting ramets, regardless of whether ramets are built of single or multiple modules and regardless of genotypic identities.

It did not escape Harper's attention that the modular perspective was relevant to the analysis of life cycles and morphogenesis of a number of animals, particularly bryozoans, colonial ascidians, and hydrozoans. The sponges, however, did escape Harper's attention and remained a telling problem: they clearly weren't colonies and they weren't clearly modular. At this level, the problem was largely solved by the publication *Population Biology and Evolution of Clonal Organisms* (1985), based on a symposium held at Yale in 1982. No longer were plants and animals considered separately, and no longer were life cycles classified in the morphological terms of solitary versus colonial. For the population ecologists, it appeared that aclonal and clonal captured much of what was inherently different about life cycles composed of single versus iterated ontogenies. What unified sponges, strawberries, and sea squirts was not their morphology, but rather a shared developmental program that permitted asexual multiplication. With the problem redefined, the life cycles of such phylogenetically and morphologically diverse taxa as cladocerans, polyembryonic hymenopterans, bdelloid rotifers, aspens, anemones, and sponges could be considered together.

Population Biology and Evolution of Clonal Organisms crystallized the view that clonality *per se* must have some adaptive significance, because it has evolved independently in many taxa of multicellular organisms and because it persists alongside sexual reproduction in many life cycles. With substantial success, many of the papers in the Yale symposium focused on identifying the adaptive significance of clonality. Still, not every contributor appears to have been satisfied with the aclonal/clonal distinction. Those authors concerned primarily with demographic and microevolutionary problems embraced the aclonal/clonal distinction. Understandably, the botanists (for whom all clonal organisms are modular at some level of organization), the developmental biologists, and the paleontologists (who generally must infer clonality from morphology) vacillated among the morphologically useful dichotomy of unitary/modular, the physiologically relevant division of solitary/colonial, and the demographic terminology of aclonal/clonal.

The two most recent volumes, *The Growth and Form of Modular Organisms* and *Modular Organisms: Case Studies of Growth and Form*, are based on a symposium held by the Royal Society of London in 1985. The hardbound first volume is supposed to contain the major synthetic presentations of the meeting, with the softbound second volume consisting of papers that were originally relegated to posters, but that merited publication in their own right (some more so than papers in the first volume). These volumes once again attempt to frame the consequences of repeated ontogenies in terms of morphology, but this time replacing the solitary and colonial dichotomy of *Animal Colonies* and *Biology and Systematics* *of Colonial Organisms* with the adjectives unitary and modular. Modular organisms, according to the editors, are composed of iterated morphological units. Of course, at the extreme, all multicellular organism are modular because cells are iterated morphological units. However, the organizers of this symposium excluded this end of the modularity spectrum by requiring that participants discuss organisms in which the iterated units are multicellular. Beyond these specifications, the editors continue, "Contributors to this Discussion Meeting were given only the most general guidance to what is meant by 'modular.' "

It should come as no surprise, then, that the volumes are taxonomically and thematically wide-ranging, and that the meaning of "modular" varies from paper to paper. This often leads to terminological mayhem, particularly for the uninitiated (e.g., the first paper is titled, "Life cycles and evolution of clonal (modular) organisms"). It also reveals in almost dazzling clarity what the sponges have been telling zoophytologists and phytozoologists all along: the distinctions between solitary and colonial, aclonal and clonal, and unitary and modular do not singly capture the physiological, morphological, demographic, and genetic implications of life cycles composed of repeated ontogenies. For instance, the morphology of sponges does not reflect neatly iterated ontogenies, but the capacity of sponges for extensive regeneration and asexual proliferation indicates that their life cycles are iterated. On the other hand, repeated ontogenies are expressed at various organizational levels in the morphology of many plants (leaves, flowers, and branches), compound ascidians (zooids and systems of zooids), bryozoans (determinately growing tubuliporids), and cnidarians (siphonophores and chondrophores), yet not all include phases of clonal proliferation in their life cycles.

In the preface to *The Growth and Form of Modular Organisms*, the editors identify three fundamental ways that modular organisms differ from their unitary counterparts. The first has to do with the way that modular organisms sample their environments and is as much a result of immobility of modular elements as it is of modular construction: in sessile modular organisms, different modules of the same genet may inhabit different selective regimes, either as the linked modules of a genet grow through space, or as unlinked modules (i.e., ramets) disperse. Second, modular organisms do not segregate a finite population of germ cells early in ontogeny, whereas most unitary organisms do. Retention of a population of cells distributed throughout the soma that can differentiate into germ cells presumably ensures that ramets will be able to produce gametes. This lack of segregation, however, leaves open the possibility that somatic variants (whether they arise by mutation or intergenotypic fusion) can be incorporated into gametes and transmitted across generations. Finally, at the level of the genet, modular construction may lift the surface to volume constraints that limit size and its demographic correlates, survivorship and fecundity, in unitary organisms. To the extent that this ideal is approached by modular organisms, the ontogenetic decline in cumulative reproductive probability or selective value that makes the evolution of senescence inevitable for unitary organisms, may be minuscule for some modular organisms. Consequently, senescence may be very difficult to detect, at least in terms of the longevity of most human research programs.

That most of these distinctions have as much (if not more) to do with clonality than they do with modularity *sensu stricto* only adds to the confusion. Moreover, neither the editors nor the majority of contributors attempt to draw connections among the physiological, developmental, morphological, and demographic ramifications of modularity. There are several lucid exceptions, particularly reviews by Jackson and Coates (which synthesizes several micro- and macroevolutionary consequences of clonality), Mackie (on physiological and morphological integration in colonial animals), McKinney (on the relationships between the biomechanics of bryozoan feeding and the evolution of discrete classes of colony form), and Cheetham (a macroevolutionary analysis of branching form and biomechanics in bryozoans). Two fine experimental papers, both by D. J. and

R. N. Hughes, separately explore physiological scaling and the relative contributions that genotype and environment make to phenotypic variation in colony form and demography.

For the most part, however, few of the standard ecological explanations for the adaptive significance of clonality and modularity are critically analyzed, despite a conspicuous absence of empirical support and study. Most of the authors seem to assume that linked modular growth and clonality are adaptations that enable sessile organisms to exploit patchily distributed resources. Whether asexual multiplication is an adaptation to spread the risk of wholesale genet mortality is also hardly questioned. Yet, a number of recent studies provide alternative ecological, physiological, and biomechanical interpretations of fission. McFadden (1986) found that small ramets of an alcyonacean coral capture suspended particles more efficiently than larger ramets, hence grow more rapidly. Similarly, Hughes and Hughes (in the first volume) suggest that the encrusting form of many epibenthic marine invertebrates limits growth rate because the growth zone, which lies along the colony perimeter, increases as a linear function, whereas biomass increases as an areal function. In both cases, the fact that growth rate decreases with ramet size may favor fission in modular organisms, insofar as fission leads to smaller ramets, higher ramet-specific growth rates, and higher genet-specific growth rates. As Jackson and Coates note, this scenario is an oversimplification, because small ramets may have higher size-specific mortality rates, as well as fail to reach a size at which they can garner the resources to reproduce sexually. Moreover, demographic performance in modular organisms is probably age- as well as size-dependent (e.g., Hughes and Connell 1987).

The connection between size and age in determining the demographic performance of modular organisms is one clear indication of the need to synthesize demographic and physiological studies. Another clear example is in the confusion shown by many of the authors on how indeterminate growth and reproductive potential affect the evolution of senescence in modular organisms. The onset and intensity of senescence evolve in response to the rates at which reproductive probability distributions (or selective values, *not* reproductive values) eventually decline with age. The rate at which this decline occurs will depend on the number of modules composing a genet, their morphological and physiological—hence demographic—interdependence, and size-specific growth rate.

To set matters straight, the potential for indeterminate growth does not distinguish modular from unitary organisms (or even clonal from aclonal organisms). Many unitary organisms such as fishes have indeterminate growth. The question is do size-specific metabolic and growth rates vary in qualitatively different ways for clonal compared to aclonal organisms? At the level of the module and ramet, it is doubtful that modular organisms escape the constraints of Kleiber's rule (i.e., that metabolic rates scale as $(\text{biomass})^{0.75}$). At the level of the genet, particularly genets composed of physiologically and morphologically independent modules, some of the metabolic constraints on mass-specific growth rates may be less stringent than for unitary organisms. Only the paper by D. J. and R. N. Hughes addresses this critical issue. In an encrusting bryozoan, mass-specific **respiration rate** is independent of colony size (hence there is no intrinsic physiological constraint on growth rate). Nevertheless, the implication that modular forms may escape Kleiber's constraints, hence achieve near maximal **growth rates**, is at best an approximation for organisms whose structure and performance depend on modular integration. And, even if metabolic rate and growth rate prove to be size-independent in other modular organisms (a dubious proposition), Williams (1957), Hamilton (1966), and Caswell (1985) all showed that in the best of circumstances, so long as there is a soma, iterated ontogenies are probably not completely immune to the evolution of senescence.

The level and regulation of modular integration affect the demography, behavior, and consequently the morphology of modular organisms in other ways. For example, endogenously controlled death of older modules (inappropriately termed 'senescence' by some authors) may be nothing more than a redistribution of resources that allows increased growth of younger distal modules. This reallocation may promote growth of the genet into more favorable environments, enhance local competitive ability, and allow defensive reinforcement in threatened regions of the genet. Which, if any, of these alternatives favors controlled death and fragmentation awaits both the characterization of the environment at spatial scales relevant to module size (this will change as better micro-sensor technology invades physiological ecology), as well as the analysis of demography at the level of the module, ramet, and genet.

The branching architecture characteristic of many modular organisms, and the apparent response of branching pattern to environmental heterogeneity, suggest that relatively simple rules of growth may underlie apparently complex morphologies. Attempts to reduce the structural complexity of modular organisms into iterated rules of growth have primarily taken the form of computer simulated models of stationary branching processes. Although these deterministic models of branching have become more sophisticated in their approximations of morphological patterns (see Bell's contribution), Steingraeber and Waller caution that branching patterns in many trees are nonstationary. It seems a safe assumption that this is also the case in many arborescent, modular marine invertebrates. To the extent that branching patterns vary ontogenetically in their bifurcation ratios, approaches using time-variant scaling of growth (e.g., fractal geometry) will be a great boon to descriptive morphology.

The application of fractal geometry to the analysis of growth and form also promises to broaden our insights as to how modular architecture is endogenously and exogenously controlled. Over the last twenty years, botanists have made substantial progress toward untangling the physiological complexities of endogenous regulation of modular growth and behavior. The excellent review by Mackie (with an especially elegant description of locomotion in siphonophores) demonstrates that zoologists are considerably farther behind. Species which endogenously fragment such as numerous soft corals, sponges, and colonial ascidians would make superb experimental models for such work.

Much remains to be done in terms of understanding how genetic, biotic, and abiotic processes regulate the development and morphology of modular organisms. One of the more conspicuous morphological correlates of iterated ontogenies is modular polymorphism. How does a single genotype produce such diverse phenotypes? Gottlieb correctly diagnoses that virtually nothing is known about the genetic contribution to variation in growth patterns in modular organisms, although the paper by D. J. and R. N. Hughes (in the *Case Studies* volume) is a notable empirical exception. On the biotic side, Dyrynda examines the effects of predation on the evolution of defensive polymorphisms in sessile, modular animals. Franco's analysis of the relationship between levels of physiological integration and growth response under competition is one of the few papers in the symposium that includes substantial references to both the botanical and zoological literature. He suggests the expected, namely that modular organisms which are strong interference ("phalanx") competitors show higher levels of modular integration than exploitative ("guerilla") competitors. Although there are several studies that investigate the abiotic effects of nutrient distribution on growth patterns in modular animals and plants, there is a dearth of studies on the responses of plants and animals to air and water movement. Thigmomorphogenesis (the developmental effects of mechanical perturbations on growing tissue) is known to have dramatic effects on plant architecture. The mechanisms of induction of the regulatory molecules causing thigmomorphogenesis is now being studied in several botanical systems. The comparable effects of fluid motion on developmental and demographic plasticity have been only superficially explored by zoologists.

The ontogenetic structural iteration that endows modular organisms with extraordinary phenotypic versatility and plasticity also seems to predispose them to the proliferation and transmission of somatic variants. These genetic variants may gain access to a genet's life cycle through somatic mutation, pathogenic infection, or, in the case of substratum-bound clonal invertebrates, by intergenotypic fusion of conspecifics. (Root-grafting occurs in some plants, but the genetic distinction between somata usually remains distinct because plant cells are immotile.) Whitham and Slobodchikoff (1981) first suggested that somatic variation could confer substantial ecological benefits because a chimerical individual potentially has a broader genetic spectrum of pathogenic and herbivore defense. Buss (1982), however, noted that because clonal organisms (including meristematically growing plants that probably do not clone) generally do not sequester a germ plasm early in ontogeny, genotypes also face the risk of competition between genetically distinct cell lineages for positions in the germ line. Such competition may have favored the evolution of mechanisms that restrict the potential for intergenotypic fusion (e.g., somatic compatibility systems) and that control the proliferation of deleterious variants (e.g., cell cycle synchronization and immune systems). In *The Growth and Form of Modular Organisms,* Hardwick argues that diplontic selection in plant apical meristems eliminates those somatic variants that could destabilize ontogeny, an idea strikingly similar to Buss'.

These problems, like that of species selection (an issue tantalizingly raised by Jackson and Coates, who found that the geological durations of clonal and aclonal scleractinian coral species do not differ), require analysis of the relative importance of selection at different hierarchical levels. In the case of somatic variation, some preliminary theoretical studies (e.g., Slatkin, 1985) suggest that selection among genetically heterogeneous meristems and branches will be considerably weaker than selection at higher levels. At this point, the data are too sparse and the theory too limited to evaluate whether somatic variation and somatic selection play profound roles in the life histories of modular organisms.

The greatest disappointment of these two volumes is that the implicit promises of the prefaces are never kept. There is little new ground broken, and the volumes lack much in the way of coherent and critical examination of some of the most intriguing aspects of modular organization. Many of the substantial issues raised in passing by the editors and contributors lie empirically and theoretically fallow. For example, not all modular organisms live forever, and more attention needs to be given to the causes of evolved variation in longevity. That modular organisms can live much longer than unitary organisms seems clear enough. Some of the implications of extraordinarily long lifespans for the attainment (much less the recognition) of evolutionary equilibrium have been raised by Potts (1984), but not subsequently extended.

With the exception of a few papers, the genetic control and the genetic consequences of modularity and clonality are largely ignored. In developmental terms, this is ironic because modular organisms—particularly those with polymorphic modules—provide some of the best opportunities for sorting out the relationships among genotype, environment, and differentiation. This paucity of genetic data, particularly regarding the dispersion, density, and diversity of genets (and not just ramets), also limits our ability to weigh the contributions that sexual reproduction and asexual multiplication make to the genetic structure of populations of clonal organisms. Several of the papers reiterate the subtle ways that sedentary modular organisms behave. But only one of the papers considers how the relatedness of interacting modules, ramets, and genets can determine whether conditional behaviors such as aggression and defense, fusion, morphological plasticity, and resource shunting enhance or decrease fitness at the level of the genet. Finally, one of the least understood correlates of modularity, the potential for natural selection to occur within somata is conceptually plausible, but the frequencies of chimeric individuals, and the distribution of selectively important variation within and among individuals, are unkown.

Despite the deficiencies of the Royal Society volumes, the publication of some new data and the iteration of previous issues may serve to clarify what needs to be done next, and even provide the inspiration to do it. Before more generalities are sought, symposium organizers would do well to focus attention on specific implications of modularity (or coloniality or clonality) such as physiological and biomechanical scaling, communication, behavior, life-history evolution, population genetics, and selection at the level of cells, individuals, species, and higher grades of organization. In the meantime, organisms with iterated ontogenies will continue to be worth studying in their own right, not just because they may be different from unitary organisms, but because of the insights they are certain to provide into problems ranging from the regulation of differentiation and physiological integration, through the relative importance of different levels of selection, to the micro- and macroevolutionary significance of sexual reproduction.

Literature Cited

BOARDMAN, R. S., A. H. CHEETHAM, AND W. A. OLIVER, JR. (eds.). 1973. Animal Colonies, Development and Function through Time. Dowden, Hutchinson, and Ross; Stroudsburg, Pennsylvania.

BUSS, L. W. 1982. Somatic cell parasitism and the evolution of somatic tissue compatibility. Proceedings of the National Academy of Sciences U.S.A. *79*:5337–5341.

CASWELL, H. 1985. The evolutionary demography of clonal reproduction. Pp. 187–224. *In* Jackson, J. B. C., L. W. Buss, and R. E. Cook (eds.), Population Biology and Evolution of Clonal Organisms. Yale University Press; New Haven, Connecticut.

HAMILTON, W. D. 1966. The moulding of senescence by natural selection. Journal of Theoretical Biology *12*:12–45.

HARPER, J. L. 1977. Population Biology of Plants. Academic Press; London.

HUGHES, T. P., AND J. H. CONNELL. 1987. Population dynamics based on size or age? Some demographic consequences of partial mortality, fission, and fusion. American Naturalist *129*:818–829.

JACKSON, J. B. C., L. W. BUSS, AND R. E. COOK (eds.). 1985. Population Biology and Evolution of Clonal Organisms. Yale University Press; New Haven, Connecticut.

MCFADDEN, C. S. 1986. Colony fission increases particle capture efficiency of a soft coral: advantages of being a small colony. Journal of Experimental Marine Biology and Ecology *103*:1–20.

POTTS, D. C. 1984. Generation times and the Quaternary evolution of reef-building corals. Paleobiology *10*:48–58.

ROSEN, B. R., AND G. LARWOOD (eds.). 1979. Biology and Systematics of Colonial Organisms. Academic Press; London.

SLATKIN, M. 1985. Somatic mutations as an evolutionary force. Pp. 19–30. *In* Greenwood, P. J., P. H. Harvey, and M. Slatkin (eds.), Evolution: Essays in Honour of John Maynard Smith. Cambridge University Press; Cambridge.

WHITHAM, T. G., AND C. N. SLOBODCHIKOFF. 1981. Evolution by individuals, plant-herbivore interactions, and mosaics of genetic variability: the adaptive significance of somatic mutations in plants. Oecologia *49*:287–292.

WILLIAMS, G. C. 1957. Pleiotropy, natural selection, and the evolution of senescence. Evolution *11*:398–411.

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Paleobiology, 15(1), 1989, pp. 73–78

Review

The Whole Real Guts of Evolution?

Genetics, Paleontology, and Macroevolution. Jeffrey Levinton. Cambridge University Press; Cambridge. 1988. xiv + 637 pp. $37.50.

Levinton's title recalls the 1949 volume *Genetics, Paleontology, and Evolution,* edited by Jepsen, Simpson, and Mayr. The 1949 volume was a landmark, one of the fruits of a confluence of evolutionary thought that also produced the Society for the Study of Evolution and its eponymous journal. In evoking this title, Levinton seeks the same kind of concordance that, forty years ago, reflected the synthesis of these three disciplines into what eventually became the neodarwinian thought of the 1950s and 1960s. To say that he fails, for this reader at least, in his appointed task

0094-8373/89/1501-0010/$1.00