

Non-Weismannian Evolution^{1,2}

Leigh M. Van Valen
 Biology Dept. (Whitman)
 University of Chicago
 915 E. 57 St.
 Chicago, Ill. 60637, USA

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Weismann

What is called Weismann's dogma of the continuity of the germplasm and the epiphenomenal nature of the soma has been a fixture in textbooks probably since the late Nineteenth Century, although I haven't checked before his own evolution text of 1902. Because his theory is commonly misinterpreted, in different ways, to fit one or another later view, I summarize it here.

He viewed the material which controls development, the idioplasm, as being the chromosomes, each of which was composed of a sequence of bodies called determinants. The determinants were segregated in groups among the daughter cells at each mitosis. One determinant then became activated in each cell and released its own component units, called biophors, which passed into the cytoplasm. Biophors were groups of different kinds of molecules and were what composed protoplasm. They could replicate themselves and were the smallest physiological units; their information was more or less equivalent to their physiological activity. Cells differed because they, and their progenitors, had activated determinants different from those of other cells. The sequence of activation was itself predetermined.

Each potentially reproductive part of an organism contained undifferentiated cells which were connected to the zygote or other initiating cell by an unbroken sequence of undifferentiated cells. This sequence he called the germ-track. The germplasm, which contained copies of all the determinants, divided from the rest of the idioplasm and remained inactivated. The germplasm itself divided in meiosis (Weismann predicted meiotic reduction in each sex before it was observed) and the reduced germplasm passed unchanged through the gametes. The germplasms of the gametes united in the zygote to form the new idioplasm, or set of chromosomes.

The basic idea of the continuity of the germplasm and the ephemerality of the soma had been proposed in 1872 by Galton, and a few others had taken it up, notably Samuel Butler (1877) in his famous quip that "... a hen is only an egg's way of making another egg."

Continuity of the germplasm is not the same as continuity of germ cells, which had also been proposed by others and which Weismann argued vigorously against. His own work had dealt with the formation of germ cells in hydrozoans, where there is no discrete germ line: "The unchanged germ-plasm of the fertilized ovum then only led to the formation of germ-cells after passing through a long series of somatic cells" (Weismann 1893, p. 185). Rather, the continuity "consists in the germ-plasm of the fertilised egg-cell becoming doubled primarily, one of the resulting portions being reserved for the formation of germ-cells" (p. 200). "... germ-plasm at any rate cannot be formed from somatic idioplasm" (p. 186, italicized in original). With respect to adventitious buds of plants, "I assumed that certain series of cells which in these species take part in forming the leaves contain unalterable and inactive germ-plasm in addition to their own active idioplasm" (p. 211).

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²Population Biology and Evolution of Clonal Organisms. Jeremy B.C. Jackson, Leo W. Buss, and Robert E. Cook (editors). 1986 (copyright 1985). New Haven: Yale Univ. Press. xi + 530 pp. ISBN 0-300-03379-6 hardbound, \$60.00; ISBN 0-300-03650-7 softbound, \$30.00.

Weismann's theory included an unchanging set of chromosomal determinants, different subsets of which were predictably activated in different cell lineages. The details have been superseded but the basic form of the theory remains, despite additions such as epigenetic interactions. It is more the common caricature of Weismann's views, emphasizing the notion that the soma is ephemeral and is unimportant in evolution except as it lets the genes interact with the environment, that the phrase "non-Weismannian evolution" refers to. I apologize to Weismann's memory, but the caricature is circulated under his name.

Even the caricature does seem to apply to the animals most familiar to us: vertebrates, arthropods, mollusks, echinoderms, and others. Weismann demolished the common-sense view of the inheritance of acquired characters, and the caricature buried it deep in a polluted landfill. (Oddly, by 1902 Weismann did accept environmental induction into germplasm, calling it induced germinal selection.)

Conceptual revision

We threw too much out. There is another world untouched by the caricature (which has never been in vogue among botanists), a more general world which undermines the rigidity of the caricature even where it seems to fit. In this world individuals often don't have obvious boundaries, reproduction is often asexual, growth and persistence can partly substitute for reproduction, and so on.

And it makes a difference in some of our most basic evolutionary concepts. The difference is real, and it affects real processes at a deep level. In addition to the awkwardness with individuality, the non-Weismannian world is where most problems with the nature of species occur. These difficulties have long been recognized, even if often swept under the rug. The more severe problems with fitness are not yet widely known. The same is true for generation length, time scales of selection, levels of selection, population regulation, the substance of demography, life-history theory, symbiosis, the topology of phylogenies, inducible variation, transmission of acquired characters, and senescence. The list is undoubtedly incomplete, and the book considers several of the topics. Clear thinking is especially important, and difficult, in areas where our received concepts tend to distort our views of the structure and processes which occur there. I therefore preface my discussion of the non-Weismannian world with an undoubtedly boring, but nonetheless necessary, digression on terminology.

Terms

There are several partly conflicting terminologies in use; none have much of a history and each is incomplete. Without hoping to impose uniformity I nevertheless make a proposal; I think that each distinction in it is one that should be made, whatever names for them prove durable.

Module: One of a set of repetitively homologous structures which jointly can or do make up all or part of a larger unit and which is, or once was, connected to another module or a progenitor of modules. Even a parthenogenetically-produced aphid is a module, with various sorts of other modules inside it.

Individuoid: A module which has at least most of the structures of an isolated individual.

Ramet: One or more modules which can or do live separate from others.

Synramet: A ramet with more than one module (which may itself be an autoramet) mutually connected.

Autoramet: A ramet with only one module.

Automodule: A module unconnected to others.

Genet: A zygote plus each of its cell lineages until the lineage is interrupted by another fertilization (or by other joining of genomes: parasexuality, endosymbiosis). Thus haploid gametophytes are included in the same genet with their diploid progenitor; perhaps they should not be. For completeness, parasexuality and endosymbiosis should initiate a new genet too; perhaps this should also happen with

hypermutilism.

Hypermutilism: Mutilism in which the partners act as an ecological unit or individual. Examples: lichens, green hydras, planktonic and large foraminiferans, hermatypic corals, mycorrhizal associations, killer parametia (a mutilism when in an environment with both partners).

Syngenet: A genet which has all of its parts (except gametes) structurally connected.

Diagenet: A genet in which some of its parts are structurally separate.

Autogenet: A genet without ramets.

Colonoid: A structurally connected group of individuals.

Eucolonoid: A colonoid in which the individuals are physiologically integrated.

Pseudocolonoid: A colonoid with only structural connection among its individuals.

Colony: An integrated group of automodules or autogenets.

Reproduction: Production of a new ramet or genet.

Clone: A genet which includes two or more ramets.

Subclone: A reproductively connected segment of a clone.

Cytoclonet: A cell and its descendants in all cell lineages except where a lineage is interrupted by meiosis, fertilization, parasexuality, or endosymbiosis. A cytoclonet can be one autoramet, part of one, several, or part of one plus all of others.

Polygenerate: An organism which can reproduce at more than one part of its body.

Clonate: An organism which can reproduce by cloning.

Somatogen: A polygenerate or a clonate; an organism which lacks a specific germ line from which all reproduction occurs sexually.

Gonogen: An organism which has a specific germ line from which all reproduction occurs.

Adjectives are obvious for each term, e.g. "rametal", "colonoid", "polygenerative". Boundaries between most adjacent concepts are fuzzy, but that does not make the distinctions less useful than those of green from yellow or youth from maturity. I am avoiding use of the word "individual" in the non-Weismannian universe because it has several defining criteria, none of which is paramount in normal usage and which covary poorly. It can refer to most of the above-defined concepts, but it is nevertheless sometimes useful when ambiguity is legitimate or when it is suitably modified (as "a physiological individual").

Now there is real biology to consider. Take demography and life histories. While it isn't quite true that, as the editors claim, "all previous life-history theory is based on the analysis of age-dependent processes" (p. x, italics in original), the claim is close enough to strike home when one realizes that size and condition tend to be more important than age in somatogenic organisms. (Johnson and Cook [1968] and Maiorana [1976] are examples of earlier work, even on gonogenic organisms, to take this approach.) In the book Caswell and Cook discuss demography and several papers deal with aspects of life history.

Two main strategies have been described for resource competition by clonal organisms, appropriately called the phalanx and guerilla strategies. A third, by the same analogy, would be scattershot, as with strobilization. The second and third strategies tend to avoid the susceptibilities of a monoculture. Local environmental stresses can elicit local responses, as in (nonclonal) trees, where growth of a branch depends on its own photosynthetic contribution, but response can be more general also. A major advantage of somatogens is their potential for adaptive flexibility, in part also by the repetition of modules in a variably adverse environment. The optimal strategy of branching varies greatly in different circumstances, as Waller and Steingraber indicate.

Senescence

The evolutionary explanation of senescence receives striking confirmation from somatogens, a result which is approached but not reached by several authors (and, e.g., by Carr and Pate, 1971). Pleiotropy which benefits the young at the expense

of the old is advantageous only when the old have a lower reproductive value, which especially for somatogens requires a careful look at the nature of fitness. One critical point is that the germ line never senesces. If it did, any such lineage would itself die of old age. This fact immediately disposes of all biochemical and physiological hypotheses which invoke automatic, necessarily acting causes; they would apply to the germ line also. Even if their effects can be reduced in the germ line a progressive, if slower, deterioration would be expected over time in the lineage (like Muller's ratchet for asexuality) because (unlike Muller's ratchet with positive mutations) the necessarily occurring deterioration would not be reversed. In most somatogens there is no specific germ line at all, so it would be difficult even to channel senescence appropriately.

And there are classes of organisms which don't senesce. All seem to be somatogens (Molisch, 1938; Comfort, 1979). Unicellular organisms don't senesce except for most ciliates, where the amitotic macronucleus progressively degenerates until it is reconstituted after a new fertilization. (And many diatoms have an analogous problem, the new test being smaller than the old one.) Sponges, reef corals, sea anemones, worms which can regenerate themselves or reproduce asexually, and perhaps all iteroparous plants are multicellular examples; many groups have not yet been studied from this perspective.

Semelparous organisms (including unicellular ones) of course senesce for adaptive reasons, but this is a rapid phenomenon unlike the slow deterioration of most gonogens. (The evolutionary selection principle is nevertheless the same.) Some somatogens, like most trees, eventually increase their probability of death merely because of size-related effects (e.g., surface-volume, wind resistance, emergence from canopy, or height, volume, or weight themselves) or by accumulation of parasites, not endogenous intracellular degeneration. The apparent aging of trees is reversible by grafts to younger ones (Wareing and Seth, 1967; Watkinson and White, 1985; but see Molisch, 1938). The loss of viability of seeds with age presumably reflects their use of stored resources and effects of dehydration and the like (Wareing and Seth, 1967), while the "senescence" of leaves, root hairs, and other disposable parts (even sometimes the whole shoot) is a directly adaptive process at the level of the entire individual and resembles our shedding of cells from various epithelia. Some somatogens are (ameiotically) gonogenic and show senescence of ramets (Bell, 1984).

Senescence can be induced in some amoebae by starvation, and the effect is then heritable (Muggleton and Danielli, 1968). The fungi Podospora and Aspergillus senesce, while Neurospora does not (Holliday, 1969). Although details are partly unclear, it is perhaps relevant that of these three genera only Neurospora does not regularly reproduce sexually. Something must nevertheless keep senescence from accumulating over time in every lineage, sexual or asexual. And older individuals of some bryozoans and colonoid hydroids progressively die (Palumbi and Jackson, 1983), perhaps to aid the growth of the colonoid, as may be the case for a similar phenomenon with aspen clones. Such cases need detailed examination from both mechanistic and adaptive viewpoints. It nevertheless is probably the case that somatogens do not undergo endogenous senescence unless there is a special circumstance which makes it adaptive to do so.

Levels

Environmentally induced variation in clonates can to some extent be transmitted in reproduction with no violation of the Central Dogma. This is obvious and well known, if perhaps not really assimilated. Equally obvious, and probably less well known, is the potential for permanent incorporation of somatic mutations in the offspring of polygenerates. Two aspects of this deserve mention. Mutations which will be incorporated are only those in cell lineages which will give rise to gametes or clones, and so the number available is not increased much if at all over that in gonogens. On the other hand, when there is local control of proliferation there is a real possibility for the occasional testing of mutations before their

incorporation into gametes. This requires an early enough occurrence in growth for the relevant meristem or equivalent to produce enough soma to be selectable and for it also to give rise to reproductive structures or areas.

Standard theory measures time in generations. Here we run head on into the conflicting criteria of individuality. In some interactions and processes a ramet acts like a gonogenic individual; in others it doesn't. A direct solution is to measure time by a clock; it is after all on this scale that real interactions occur.

Similarly, the standard theory of population regulation counts individuals. But it can hardly be the case that natural processes depend on how we define terms, and a large individual is not equivalent to a small one (or an active one to one in dormancy). It is therefore essential to eliminate counts of individuals from this theory; energy flow is the only universal and natural replacement.

In one sense a species is equivalent to a clone if sexual reproduction is rare enough, and clones and species interact in similar ways. However, as Sebens and Thorne discuss in the book, there are differences even here. In another and more usual sense a species is equivalent to a cluster of clones. In a third sense obligate clonates lack species. There is more to say here, but I merely note that the concept of levels of selection itself becomes blurred. The same is true at the level of the individual, where different criteria also go with different processes. How, exactly, does individual selection differ from group selection for a clonate? Or from within-individual selection? Clonates interact with nonclonates too; these questions are not primarily ones of terminology. We must therefore recognize that levels of selection intergrade with each other. Even if there were no other reason to do so (and there are others, both up and down), this conclusion forces us to look skeptically at the usual view of individual selection as the overwhelmingly most powerful level.

In the book Buss provides a extensive comparative review of some aspects of selection within individuals. He regards the repeated evolution of aclonality as an adaptation to suppress the proliferation of somatic variants. That argument doesn't hold for plants, though, and the subject needs more work. In two papers, one with Coates, Jackson gives evidence for the frequently adaptive nature of clonality and its attributes. They seem surprised, though, that individuoids (unlike gonogens) show no evolutionary trends for increase in size. The comparable unit here, though, is presumably the colonoid, for which they give no data.

Wulff argues reasonably that clonality helps in the origin of mutualistic interactions, and Pitelka and Ashmun discuss connections between plant ramets. But hypermutualism raises problems too. The integration of an endosymbiont is a gradual process; when do two lineages become one? Intermediate stages seem to persist sometimes for long periods. The same question can be asked for other hypermutualisms. A lichen acts ecologically as a single species; it even has its own morphology. Have lineages merged here? If we consider all the processes which are relevant, some fall on one side and some on the other. The only non-arbitrary answer is, "partly". Our question was not one which permits a precise answer, and we should adjust our thought to conform to real processes rather than trying to force them into predefined boxes.

Fitness

Somatogens are among the nonstandard but common entities to which the usual view of fitness doesn't apply naturally. At least I suppose there is a usual view of fitness -- it seems almost as though everyone who considers the concept seriously emerges in a different place. This divergence of opinion is symptomatic of a genuine and deep problem at the foundation of our science.

The problem isn't one of convention. Every instance of natural selection has a definable outcome, and our task is to find what it is that natural selection maximizes (or minimizes). It is always basically the same process; at least we know that by now. It should always operate by the same underlying rules.

The usual population-genetic view is that fitness is the relative number of

offspring in the next generation. Every aspect of this definition can be undermined. It is easy to construct examples, and there are probable real cases, where one variant increases in relative frequency but causes its population to go extinct. Thus from a broader view fitness must be something absolute, in a particular environment.

Similarly, use of generations as a measure of time is awkward at best in the continuous case, and it becomes downright unrealistic when competitors have different generation lengths, as they usually do. It is also commonly realized, when it is thought about at all, that selection on a short time scale can and often does lead to results which are detrimental on a longer time scale. Selection acts on all time scales; none is preferred or privileged.

Up to this point the problems and solutions are often recognized if not often implemented.

It is the remaining parts that somatogens help to undermine. We have already seen the nonequivalence of large or active individuals with small or dormant ones. The same is true at levels of groups: e.g., a lineage with one abundant species is not thereby necessarily less fit at any time scale than a lineage with several rare species. The currency of free energy provides a uniformly available measure which, moreover, acts causally in the relevant biological interactions.

Both somatogens and groups exemplify a component of fitness which is not obvious for gonogenic individuals. This is expansion (including negative expansion, or contraction). A plant or a coral ramet may grow out, or it may put the same energy into sending forth a new ramet, or into sexual reproduction. A group may enlarge or it may split. These alternatives are mutually equivalent for immediate fitness, although their consequences may differ on one time scale or another. Expansion can in fact be regarded as the basic aspect of fitness, for reproduction and survival can be included in it with little difficulty.

Somatogens and groups also show another unfamiliar aspect of fitness, namely persistence. They don't senesce, usually, so they can potentially remain as the same unit indefinitely. A plant is not automatically more fit by reproducing and dying, so that its offspring can occupy its site or the equivalent, than it is by just staying where it is. Of course, if it doesn't reproduce at all the slings and arrows of outrageous fortune will eventually impale it, but that is a comparison on a different time scale.

It is therefore possible to agree with Buss's more narrowly based conclusion that ". . . an expansion of the theoretical underpinnings of the modern synthesis merits consideration" (p. 498).

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