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Evolution

Evolution, development, and the units of selection

(epigenesis/Modern Synthesis/preformation/somatic embryogenesis/Weismann's doctrine)

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ABSTRACT **The "Modern Synthesis" forms the foundation of current evolutionary theory. It is based on variation among individuals within populations. Variations within individuals are believed to hold no phylogenetic significance because such variation cannot be transmitted to the germ line (i.e., Weismann's doctrine). Weismann's doctrine, however, does not apply to protists, fungi, or plants and is an entirely unsupported assumption for 19 phyla of animals. This fact requires that the Modern Synthesis be reexamined and modified.**

The Darwinian notion of evolution as a process directed by selection acting upon heritable variation has not been challenged seriously since Darwin first articulated it. The logical structure, however, of Darwin's argument leaves open the question of which unit(s) of biological organization selection acts upon. As Lewontin (1) and others have pointed out, any unit of biological organization capable of (*i*) self-replication with high fidelity, (*ii*) heritable variation with equivalent fidelity, and (*iii*) selection acting upon variants is a unit capable of evolution. The past century has seen repeated debates as to which units of biological organization are units of selection and which units of selection have been of primary importance in determining the major features of evolution (1–3).

Much of the current emphasis upon the individual as the principal unit of selection can be traced to the enormous influence of the famous 19th century zoologist, August Weismann. Weismann's major contributions spanned the two decades from 1872 to 1892. The period was a turbulent one. Darwin's great synthesis was largely accepted in many biological circles, yet Mendel's observations and their consequences had yet to be widely appreciated. The ideas of Lamarck, bulwarked by Darwin's "pangenesis" notions, were still afloat, particularly in botanical circles. The study of evolution, though flourishing, seemed to be limited to careful comparative anatomy and the excited exchange of promised correlations among adherents.

Weismann's major contribution was his "doctrine of the continuity of the germ line" (4). The doctrine dealt a final blow to adherents to Lamarckianism and, for the first time, articulated a clear statement as to the units of selection. Weismann (4) argued that there existed a "molecular basis" for a distinction between the germ plasm and the soma such that heritability was solely the province of the "germ plasm" and that the soma was simply a mortal vessel of no evolutionary significance.

Falsification of Weismann's doctrine was quite impossible in the 19th century, yet his views became broadly accepted. Three trends were of utmost importance here. First, many botanists and zoologists, disturbed by the lack of clear evidence in favor of a Lamarckian "inheritance of acquired characteristics" or of Darwin's pangenesis notions, found in Weismann's doctrine a clear and simple explanation. Secondly, zoologists, particularly those working with the comparative embryology of vertebrates, saw strong evidence for Weismann's scheme in the sequestering of germ cells during early embryology. Finally, several investigators studying wound-healing had clearly illustrated that many somatic cells were, in fact, incapable of regeneration.

Support for Weismann's doctrine was by no means universal. Botanists were Weismann's earliest critics (5). Debate over the issue was central in the development of the continuing rift between botanists and zoologists despite the commonality of their interests (G. E. Hutchinson, personal communication). Although Weismann's doctrine was the subject of two very critical reviews in the 20th century (6, 7), these criticisms fell on deaf ears amongst the excitement surrounding the new field of genetics, and Weismann's doctrine became dogma.

In this paper I summarize data from the literature that clearly illustrates that Weismann's doctrine is, at best, an unsupported assumption for most organisms. This fact (*i*) required recognition of suborganismal units of biological organization as units of selection, (*ii*) clarifies the role of development in evolution, and (*iii*) calls for reexamination of both the "Modern Synthesis" and current macroevolutionary theory.

EVOLUTION AND DEVELOPMENT

Evolutionary theory treats reproduction as falling into two categories: sexual and asexual. Sexuality is generally considered to be equivalent to meiosis or prokaryotic conjugation, and asexuality, to represent binary fission, mitosis, or ramet production (i.e., whole organism cloning through budding, spore formation, microcysts, gemmules, statoblasts, rhizomatry, etc.). These are all treated as replicatory events that occur at the level of the individual and do not include many other modes of replication that are known to occur. For example, the asexual reproduction of cells within a multicellular organism are considered to have no phylogenetic significance except as they may contribute to the survivorship and fecundity of the individual.

Concentration on reproduction at the level of the individual is justified by a belief that the sole unit of selection is the individual. This tenet is viable only if (*i*) suborganismal replication does not occur, (*ii*) suborganismal replication produces no variability, or (*iii*) suborganismal variability is not heritable (1). The first two conditions are clearly false, and the validity of the final condition is dependent upon the validity of Weismann's doctrine.

The validity of Weismann's doctrine is a function of the extent to which cells in a developing organism become irreversibly determined to some purely supportive role (4). Although genetic variants commonly arise within genomes, organelles, and cells, such a variant will not be heritable if it is (*i*) denied access to the formation of gametes or (*ii*) denied the capacity to asexually form an independent new organism capable of further propagation, or denied both. Two sets of processes determine the potential for propagation of somatic variants: the sequestration of primordial germ cells and the irreversible differentiation of somatic tissues.

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As pointed out a century ago, a clear distinction can often be drawn between the germ line and the soma (4). In many animals, cells in the early embryo undergo a series of morphogenetic movements leading to their becoming lodged in a given tissue. Here they lie quiescent, contributing in no way that can be recognized by current histological and immunological techniques to the maintenance of supportive functions. At reproductive age, these cells, and these cells alone, form the gametes. For any organism whose germ cells are set apart in this way, the opportunity for the propagation of somatic variants is severely limited. If the variant does not arise during those first few cell divisions prior to the sequestering of primordial germ cells, the germ–soma barrier will prevent its propagation.

Table 1 presents a compilation of those organisms in which sequestering of germ cells is documented. Two patterns are clear: (*i*) sequestering is a phenomenon limited to the animal kingdom, and (*ii*) sequestering is not found in those animals capable of propagation by the production of ramets. The totipotency of meristematic tissue in plants and the coenocytic nature of fungi makes any attempt to distinguish between germ and soma inappropriate. The association between ramet production and sequestration is equally transparent. A potentially immortal organism capable of indeterminate growth and asexual propagation could not possibly sequester all the eggs it might need throughout its life.

Direct incorporation of somatic variants into gametes is only one way in which a somatic variant might produce a new individual. In any form capable of ramet production, somatic variants incorporated into the ramet may produce a genetically distinct individual. The extent to which somatic variants may produce new individuals in this fashion is dependent upon the degree to which somatic tissues are irreversibly committed to specialized supportive roles. The issue of developmental determinism in somatic cell populations is a critical one. A somatic variant which has arisen in a lineage that has already become terminally differentiated for a specific role will be unable to generate a new individual through ramet production.

Developmental biologists have long classified organisms in terms of the degree to which embryonic cells are irreversibly determined. From the data presented in Table 1, three categories can be recognized: (*i*) those organisms capable of regenerating a new organism from certain tissues at any life stage (somatic embryogenesis), (*ii*) those organisms in which at least some potentially propagative tissue remains undetermined until relatively late in development (epigenetic development), and (*iii*) those organisms in which all cell lineages are irreversibly determined in early ontogeny (preformistic development).* Two patterns are evident. First, all plants, fungi, multicellular monerans and protists, and certain sponges, coelenterates, and worms are capable of somatic embryogenesis. In these forms there is no necessary restriction to the propagation of a somatic variant by asexual means. Second, preformistic development is absent in all groups in which ramet production occurs. The correlation between developmental determinism and ramet production is to be expected. Asexual proliferation demands that at least some cells either fail to differentiate or that the differentiation of some cells be reversible.

Although the discussion of modes of development has a long history, the potential consequences of these patterns for the propagation of somatic variants have been unappreciated. The data cited in Table 1 clearly establish that suborganismal variation is heritable in a wide variety of circumstances.

* In many development texts, the terms epigenetic and preformation are used as synonyms for the terms regulative and mosaic.

Table 1. Phyletic distribution of developmental determinism*

Taxa	Development†	Asexuality‡	Sequestration§
Protoctista			
Phaeophyta	s	+/−	−
Rhodophyta	s	+/−	−
Chlorophyta	s	+/−	−
Labyrinthulamycota	s	+	−
Acrasiomycota	s	+	−
Myxomycota	s	+	−
Oomycota	s	+	−
Fungi			
Zygomycota	s	+	−
Asomycota	s	+	−
Bacidiomycota	s	+	−
Deuteromycota	s	+	−
Plantae			
Bryophyta	s	−	−
Lycopodophyta	s	+	−
Sphenophyta	s	+/−	−
Pteridophyta	s	+/−	−
Cycadophyta	s	−	−
Coniferophyta	s	−	−
Angiospermophyta	s	+/−	−
Animalia			
Placozoa	s	+	−
Porifera	s	+/−	−
Cnidaria	s	+/−	−
Ctenophora	p	−	+
Mesozoa	p	−	+
Platyhelminthes			
Turbellaria	s	+	−
Trematoda	p	−	+
Cestoda	e	−	−
Nemertina	e	+/−	−
Gnathostomulida	u	−	u
Gastrotricha	p	−	+
Rotifera	p	−	+
Kinorhyncha	u	−	u
Acanthocephala	p	−	+
Entoprocta	s	−	−
Nematoda	p	−	+
Nematomorpha	u	−	u
Ectoprocta	s	+	−
Phoronida	s	+/−	−
Brachipoda	u	−	u
Mollusca	e, p	−	+/−
Priapulida	u	−	u
Sipuncula	u	+/−	u
Echiura	u	−	u
Annelida			
Polychaeta	e	+/−	−
Oligochaeta	e	+/−	−
Hirudinea	p	−	+
Tardigrada	p	−	+
Onychophora	e, p	−	+/−
Arthropoda	e, p	−	+/−
Pogonophora	u	−	u
Echinodermata	e	+/−	−
Chaetognatha	p	−	+
Hemichordata	s, e	+/−	+/−
Chordata	s, e, p	+/−	+/−

* Compiled from 153 references, list available from author upon request.

† u, Unknown; s, somatic embryogenesis; e, epigenetic; p, preformistic.

‡ Excluding cases of secondary asexuality (e.g., parthogenesis, polyembryony).

§ +, Early embryonic sequestering of germ line present in all species; +/−, present in some species/absent in others; u, unknown.

A MODIFIED SCHEME

The various historical views of mechanisms of evolutionary change at the organismal level are diagrammed in Figs. 1 and 2. Lamarck and Darwin saw the soma and the germ line as freely communicating (Fig. 1 *Upper*). Weismann modified this view to insist that changes in the germ line could affect the subsequent production of the soma but that there exists no reciprocal relationship between the two (Fig. 1 *Lower*). Without challenging its basic assumptions, the Modern Synthesis codified Weismann's doctrine in terms of the genetics of populations. Because this present discussion, echoing the objections of a century ago, holds that Weismann's doctrine is at best an unsupported hypothesis for many groups, a slightly modified scheme is required.

A modified scheme is proposed in Fig. 2. It allows two interacting types of transmission of genetic changes to subsequent generations. In forms that sequester germ cells and that are unable to propagate by ramet production, Weismann's doctrine is most closely approximated. However, in forms in which germ cells are not sequestered or in which propagation by ramet production occurs, incorporation of variation may proceed somewhat differently. Here, the progression suggested by Weismann's doctrine may occur in the orthodox fashion (Fig. 1 *Lower*) (*i*) if there are no mutations in somatic lineages, (*ii*) if all of those somatic mutations that do occur are selected against in the somatic environment, or (*iii*) if all somatic mutations fail to be propagated in ramets. However, evolution can occur if a somatic variant is incorporated into future generations either by direct differentiation of the variant cell lines into gametes or by ramet production, or by both.

This modified scheme suggests revision of certain interpretations of the dynamics of both microevolutionary and macroevolutionary change.

Microevolution. The theoretical underpinnings of classical population genetics involve the explicit assumption of the individual as the unit of selection. Modification of its foundations will be necessary to accommodate the potential phylogenetic significance of sub-organismal variability. I briefly outline here two important modifications with respect to mutation rate and selection.

Mutation rate. An important source of evolutionary change is mutation. Although much of the variation observed among individuals is a result of recombination, recombination can only redistribute variation created by mutation. In organisms with preformistic development, all new mutations must arise in the production of a population of sequestered germ cells. This population is, by necessity, a relatively small one, and the opportunity for mutation to arise is accordingly low. With other modes of development, mutations may arise in any potentially propagative cell line; hence, the opportunity for mutation is substantially greater. It follows that the site of accepted mutations will most frequently be in somatic lineages.

An example is perhaps useful here. The average human female matures a total of 3×10^2 eggs in a lifetime. The same individual, at any given time, harbors a somatic cell population on the order of 10^{13} cells. By assuming a lifetime for each somatic cell of 1 month and a lifespan for the individual of 80 years, the number of potential mitotic divisions is on the order of 10^{16}. Further, by assuming a mutation rate per locus per division of 10^{-6} and a modest probability of 10^{-8} that the variant will survive, the frequency of a new variation arising in somatic lineage is on the order of 10^2 individuals, whereas the rate of this change arising in the germ line is 10^{-12} individual. Assuming a population density of humans on the earth today to be on the order of 10^{10}, this translates to a rate of only one mutational change per generation per locus for the entire species. This example is clearly artificial because somatic changes are excluded from the germ line in humans, but it does serve to illustrate that the potential for the incorporation of heritable novelty lies not with sexual organisms of preformistic development but with clonal organisms characterized by somatic embryogenesis.

Selection and environmental direction. The rate and tempo of evolutionary change is dependent not only on the rate of mutation but also on the relative success of mutations under the action of environmental selection. Any mutation must undergo the following sequence of events: the initial mutation, propagation, and environmental selection. However, the sequence of these events differs for organisms that lack sequestration, with consequent effects on the rate of change in response to environmental demand.

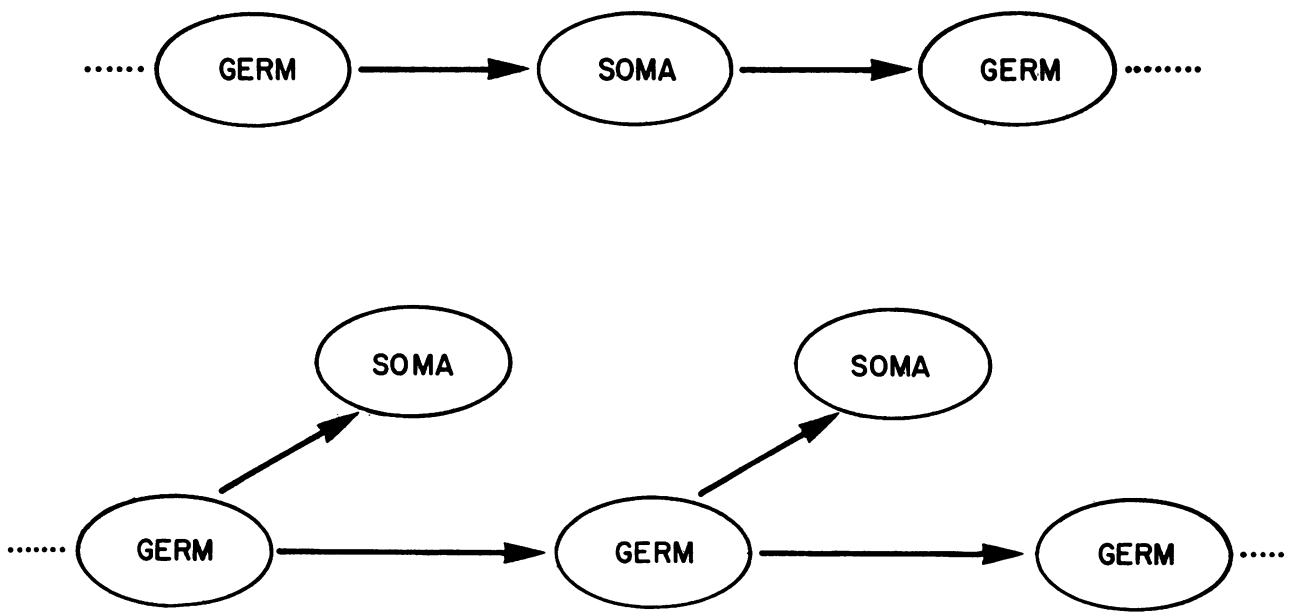

FIG. 1. (*Upper*) A schematic representation of the views of Lamarck and Darwin on the relationship between soma and germ lines. (*Lower*) A schematic representation of Weismann's doctrine.

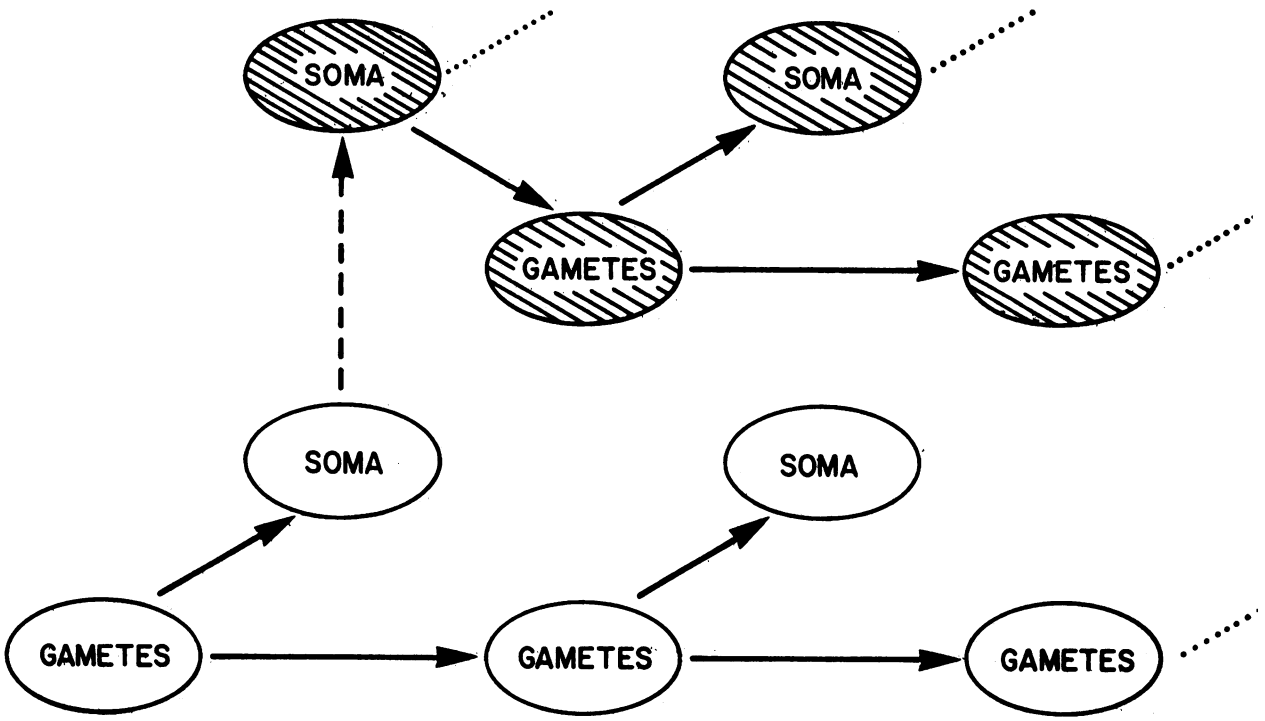

FIG. 2. A modified scheme, which allows both the mechanism proposed by Weismann (lineage without cross-hatching) and the possibility of somatic variants (--►) becoming incorporated into gametes (crosshatched lineage).

A somatic cell having undergone a mutation is immediately confronted with selection in the somatic environment. This variant will not be capable of further propagation unless it is successful in competing with other somatic cell lineages for positions in the germ line or in ramets (8). To the extent that selection in the somatic environment mimics environmental selection, the variant will be disproportionately represented in the germ line or ramets. The sequence of events for a somatic mutation is thus: mutation–selection–propagation–selection; only those mutations that survive somatic selection are propagated. In contrast, a mutation in the sequestered germ line is faced with little [e.g., gametic selection (1)] or no environmental selection prior to propagation. The sequence here is: mutation–propagation–selection; propagation in this case is random with respect to environmental demand.

Although the original mutation in either case is random with respect to environmental demand, the net effect of selection in the somatic environment is the disproportionate proliferation of those variants favored by environmental demands. This, coupled with the initially greater mutation rate, suggests the capacity for rapid evolutionary change in forms with somatic embryogenic development.

Macroevolution. The relationship between microevolutionary changes in gene frequencies and macroevolutionary changes in morphology is far from clear. Morphological plasticity on an ecological time scale is common in forms with somatic embryogenesis (e.g., plants, colonial animals, and fungi). In contrast, forms characterized by preformistic development (e.g., many vertebrates) are extremely conservative. Perhaps the most striking example is that of Korotkova's work on sponges (9), who found that species capable of somatic embryogenesis uniformly lacked a repeated colony morphology, whereas species incapable of somatic embryogenesis always form characteristic colony morphologies. Unfortunately, studies of the fossil record have not, as yet, provided similar information for geologic time scales. Existing studies with good time resolution are limited to molluscs (10, 11).

The debate between proponents of punctuated equilibrium and phyletic gradualism is focused on this issue of the rate of phenotypic divergence over time (3, 10–13). The arguments presented above suggest that organisms with preformistic development are likely to experience far less rapid rates of change than those characterized by somatic embryogenesis. If the expression of suborganismal variability results in morphological plasticity on ecological time scales, then the issue of punctuated equilibrium may be largely limited to, if not a consequence of, the preformistic developmental mode.

CONCLUSION

As recently as a decade ago, the Modern Synthesis appeared to concur comfortably with molecular biology's central dogma: DNA sequences coded for products, small sequence changes led to small product changes, and directional selection over geologic time led to divergence. However, as molecular biologists moved from the study of prokaryotes to eukaryotes, two unexpected observations were made—the presence of large amounts of repeats of DNA and the occurrence of transposable elements.

Coincident with this questioning of the mechanistic underpinning of gradual change, a second challenge to the Modern Synthesis has come from the opposite spectrum of biology. Paleontologists have long attributed the lack of fossil evidence for continuous directional phenotypic variation (phyletic gradualism) not as a pattern requiring explanation but rather as an artifact of preservational bias (12). However, in the past decade, many paleontologists have redirected attention to the issue (3, 12, 13) and, in light of recent fossil studies with good temporal resolution (10, 11), have come to accept morphological stasis over geologic time scales, punctuated by episodic changes (punctuated equilibrium) as a pattern demanding explanation.

Against this backdrop, several evolutionists have called for a revision of the Modern Synthesis and the development of a new "hierarchical theory of evolution" to accord with findings of molecular biologists, developmental biologists, and paleontologists

(3, 13). Notably absent from these criticisms, however, has been the proposal of any mechanistic basis for such a revision. The arguments presented above demonstrate a clear need for revision and provide a clear basis in development for the modified scheme. The modified scheme allows that (*i*) change at the suborganismal level is heritable and (*ii*) the extent of this heritability is regulated by the developmental processes of germ-cell sequestering and irreversible somatic differentiation.

Note Added in Proof. Two independent rediscoveries of the limitations of Weismann's doctrine have been brought to my attention. T. G. Whitman and C. N. Slobodchikoff (14), in a discussion limited to plants, raise several of the microevolutionary concerns mentioned here. P. D. Nieuwkoop and L. A. Sutasurya (15), in a discussion limited to animals, provide data that overlaps with that presented in Table 1.

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