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Tracking Organic Processes: Representations and Research Styles in Classical Embryology and Genetics

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Themes

This chapter will explore two themes concerning scientific practices, illustrated by examples drawn from research on problems of heredity and development from the late nineteenth to the early twentieth century. Because these themes apply not only to the sciences that emerged but also to the history and philosophy of science, my argument about the nature of scientific practice has historiographic as well as philosophical implications.

First, scientists frequently follow a process in order to understand both its causal character and where it may lead. Radioactive tracers, fluorescent stains, genetic markers, and embryonic transplants all facilitate tracking processes and determining how physiological, molecular, and genetic outcomes result from known inputs. Indeed, one might argue that the notion of following a process unifies descriptions of science as theoretical representation, as systematic observation, and as technological intervention.[1] Following processes is a characteristic activity of science. Moreover, the concept of science as following a process cuts across many analytical distinctions commonly used to describe science (e.g., theory vs. observation, theory vs. experiment, hypothesis-testing vs. measurement, active manipulation vs. passive observation, scientific methods vs. scientific goals). A genetic marker "marks" the transmission process in breeding experiments, but it also may be the subject of causal investigation—the role played by the marker in development or disease, for example.

Second, scientific reports of process-following tend to be accompanied by representations that reflect commitments to follow processes in particular ways, foregrounding some aspects of phenomena and backgrounding others. Visual representation of genes as causes of genetic continuity and of somatic discontinuity, for example, focuses attention on continuities the eye can follow rather than on discontinuities that must be bridged in thought.[2] Moreover, how one follows a process constrains what

one represents as followed. The representation in turn focuses attention on foregrounded elements as the significant and explanatory aspects of the process-as-followed. The result is constraint and guidance of how processes may be followed on other occasions, as well as what implications are (literally) drawn from reported work. In consequence, hereditary transmission, for example, is now hard to characterize other than by contrast with developmental expression—the causal dichotomy of the representation has become entrenched in "common sense."[3]

Finally, historians and philosophers interested in the split between embryology and genetics early in the twentieth century, after the rediscovery of Mendel's work, have tended to rely on narrative representations of the history of biology that foreground certain theories and experiments to the exclusion of others.[4] Narratives that put a single field of science in the limelight of attention at a given time constrain understanding of scientific change to occur in a linear sequence, as though genetics succeeded classical embryology rather than their branching into collateral lines of work from a common wellspring. It seems unlikely, given the social organization and realignment of scientific work in the twentieth century, that historical change would be adequately represented by a linear succession of disciplines.[5] I focus on the segmentation of lines of work early in the twentieth century that now, in evo-devo research, may be anastamosing in a process of intersection discussed by Gerson in this volume.

Since embryology is not well tracked in narratives that foreground the success of genetics after the split, succession cannot but fail to explain this episode of scientific change. We must instead follow the "bushy" divergences and reticulations of several sciences as they spawn new lines of work if we are to understand, and follow, science as a process. In my view, this means that we must follow not only the trails of changing theories and problem agendas, but also the tools, techniques, and methods for following processes which scientists deploy in their varying lines of work.

This following of scientists while they follow nature may be of some help toward assembling resources to describe and articulate the newly emerging field of evo-devo.[6] This field, comprising several intersecting lines of work, seeks to join genetic, developmental, and evolutionary research problems and programs that have been treated, quite successfully, as though they were separate throughout most of the twentieth century, but in reality they are more like the segments of a centipede: moving together with limited autonomy. It is indeed ironic that the result of this new synthesis may be the rediscovery of problems that are 100 years old.[7] Here, I follow in a line of analysts who question the origin myths of sci-

entists looking back to founding scientific fathers to explain the roots of their own fields' successes and failures.[8] In this chapter I illustrate themes of process-following, foregrounding, and backgrounding by interpreting Mendel as a developmentalist in order to reveal the extent to which workers in the late nineteenth century sought a unified account of heredity, development, and evolution. My rhetorical aim is to cultivate a new perspective on our contemporary scientific landscape, a landscape in which genetics and developmental biology are considered to have very different origins, cultures of research practice, theoretical goals, and formalisms—in short, different research styles. But where previous interpreters of Mendel have related his developmentalism to nineteenth-century concerns with the stability of species, I seek to articulate a view of Mendel as an exemplar for those modern biologists who seek theoretical unification or intersection of domains segmented by earlier generations who took Mendelism to be the "wedge issue" of the day.

The bulk of the chapter is concerned to formulate a view of Mendel's activity that may help reorient our modern understanding of genetic research styles which have come to stand in contrast to embryological and morphological research styles. The broader goal is to provide insight into developmental research styles by indicating features shared with Mendel in following processes and drawing inferences about earlier stages in terms of later ones. The paper considers embryological research styles more with an eye toward formulating problems for further research than with presentation of firm conclusions of immediate use to the interpretation of evo-devo in the light of history.

On Following a Process

Following processes is a key project for understanding causality in the world. Where, when, and how processes originate; what interactions happen to them along their way; and how they terminate is, in a word, what there is according to process ontologies. Regardless of the metaphysical standing of process ontologies, there is no doubt that scientists do follow processes, that this is an important and central activity in their work, and that they achieve causal understanding as a result of doing it.

The connection between following a process and causal understanding has long been explored by philosophers of science, though mainly by those concerned with the physical sciences. From the 1920s, Reichenbach used a "mark principle" to describe the causal relevance of factors in explanations of physical effects such as the propagation of light.

"A mark," Reichenbach wrote, "is the result of an intervention [in a process] by means of an irreversible process."[9] The mark principle helped Reichenbach articulate a technical, probabilistic criterion of causal relevance. His goal was to use the irreversibility of marking processes to infer the direction of time in marked causal processes.

My use of Reichenbach's mark principle here is not aimed at ontological problems as general as the direction of time, but rather is a tool with which to describe what biologists do when they follow processes. This is no mere analyst's category. Biologists, especially the embryologists I discuss below, often described their work as introducing and then following "marks" in order to establish the fate or prospective significance of marked parts of a dynamic process.[10] A shared assumption of genetic and embryological research styles is the notion that hybrid organic material (whether naturally or artificially produced) can serve both as the introduction of a mark into a process to facilitate tracking and as a causal intervention to see how the process might turn out differently than it otherwise would. That is to say, paying attention to particular aspects or properties in order to follow a process, marking interventions, and analyzing the causal character of a process in terms of counterfactual support may all be entwined in a single activity.

Reichenbach noted that marking interventions can be either "deliberately performed" or the product of "natural causes."[11] This distinction is relevant to the history of biology, where both experimental and observational means of marking organic processes are exploited, often in the same study, to achieve causal understanding of development in embryological and genetical research styles, as I will describe below.

Salmon elaborated Reichenbach's principle in a criterion of "mark transmission" to serve his analysis of causal processes:

> MT: Let P be a process that, in the absence of interactions with other processes, would remain uniform with respect to a characteristic Q, which it would manifest consistently over an interval that includes both of the space-time points A and B ($A \neq B$). Then, a mark (consisting of a modification of Q into Q′), which has been introduced into process P by means of a single local interaction at point A, is transmitted to point B if P manifests the modification Q′ at B and at all stages of the process between A and B without additional interventions.[12]

If a causal process from A to B can be thought of as the "development" of A, then this very abstract notion of causality contains the philosophical root problem of heredity/development. Heredity concerns the

respect in which A stands in a certain causal relation to B, while development concerns the bringing about of B from A.[13] Both concern the very same causal process, both seek an account of causal process in terms of continuity and constancy or invariance, and both investigate it by tracking marks that identify it as a causal process.[14]

In natural histories of various sorts, biologists introduce or observe a local, irreversible mark in a process of interest by attending to a particular part of the process—for example, when ecologists follow an ecosystem by tracking a particular isotope of a circulating molecule such as CO_2 or N_2. In molecular biology, experiments often consist of introducing a mark and seeing where it ends up, such as in the Hershey-Chase experiment, which tracked the whereabouts of radioactively labeled phosphorus (P^{32}) and sulfur (S^{35}) in order to determine whether phosphorus-rich viral DNA or the sulfur-rich protein coat of a bacteriophage was the information-bearing infectious agent. These are only more systematic and disciplined versions of what casual observers do on a lazy summer afternoon when they track the flow of a river by watching the movement of a leaf floating downstream.

"Noteworthy observation" is facilitated by taking note of peculiarities that make certain parts of a process stand out and thus make tracking easier.[15] As Hans Spemann remarked in 1931, "You may well make a discovery without intending to do so, but not without noticing it."[16] Noteworthy attention in biological research often results from "mental marking," a kind of tracking that is not easily assigned to either of the traditional categories of passive observation and active experiment. It is nonmanipulative yet active work on the part of a tracker, and may serve experiment as well as observation.[17] Mental marking is an actual causal intersection connecting a natural process of interest and the scientist observing it, but it is ineffective as a means of causal intervention or control through the marking interaction.

Noticing a morphological feature (a structure, a pigment pattern, a cell in a particular location) of an embryonic region is an important type of mental marking in embryology. Noted morphological features can be tracked to where they end up several or many cell divisions or developmental stages later. One means of mental marking that emerged in late nineteenth-century embryology depended on microscope observations and camera lucida drawings: features noted in the microscope were marked on a drawing of the embryo and tracked through development via superimposed labels and arrows, resulting in a diagram that represented mark transmission/part transformation through the developmental process.

The feature noted in such cases is not itself an irreversible interaction between the observer and an embryo undergoing development but, rather, part of the natural process, and thus not a mark in Reichenbach's sense. Instead, the embryologist's noticing the feature and attending to it constitutes the marking interaction. Following the mark in attention, through continued observation and aided by techniques such as camera lucida drawing, constitutes tracking the marked process.

In cases closer to Reichenbach's discussion, biologists may physically change a property of a process "from Q to Q′." In a manipulative marking intervention, the experimenter focuses on a "target" of attention prior to the marking interaction and then introduces a mark that physically changes a property of the process in such a way that continuous mental attention is not required to track the process. This is a procedural benefit of the irreversibility of marks that Reichenbach required of causal processes. The mark can be tracked in intermittent "checkups" via subsequent observations of or interventions in the process to see if the process still carries the mark Q′. This operational notion of mark transmission thus also plays a theoretical role in identifying the process as causal. Theory and methodology are as intimately related as two sides of a coin.

In what follows, I explore the nature and representation of process-following in heredity/development with examples spanning the historical period of the split between diverging embryological lines of work and the new science of genetics. New styles for following processes, theories, and methods emerged around the turn of the twentieth century, and they illustrate the way in which representations produced as a process is followed provide reinforcing feedback that organizes attention into foreground and background concerns. Foregrounding and backgrounding of different aspects of the same biological process lead to different research styles, and since narratives tend to follow historical developments within styles, history often gives a false impression of disciplines that are separate because their theories describe different processes. The split between genetics and embryology early in the twentieth century, I maintain, occurred at the level of research styles, of theoretical commitments that facilitated the segmentation of a vision of a unified social world of biological research, not the discovery of separate realms of biological processes of heredity and development.[18]

Representing a Process as Followed

Gerson (this volume) describes research styles as "abstract commitments used to organize other, relatively concrete commitments. Styles typically

appear as general philosophical or methodological positions (e.g., focusing on structural rather than functional considerations, or preferring the construction of formal models to the detailed description and analysis of particular cases). Any such pattern of commitments can serve as the basis of a subworld or intersection." Genetic and embryological research styles package commitments to follow processes according to particular sorts of marking interactions and tracking conventions together with commitments to represent processes in particular ways.[19] Attention-guiding feedback from scientific representations results from work to honor both sets of commitments. My central claim is that because geneticists and embryologists follow the same process, their research styles are constrained to be similar in certain "underlying" ways, despite the considerable divergences we associate with those disciplines. I explain the differences that historically emerged in the split between them in terms of how their diverging representational practices drove attention to different aspects of the one process and thus supported the development of distinct lines of work. I consider several kinds of examples drawn from lines of work traditionally classified as either genetics or embryology.

In the next section, I argue that Mendel's famous work *Experiments in Plant Hybridization* is clearly a work of developmental explanation, despite its championing by twentieth-century geneticists who came to view their social world and traditions of heredity research as separated from embryological research. Mendel's commitments to developmental explanation and representation are clear and undeniable from his report of what he followed, how he followed it, and how he represented what he followed.

The seeds of a new, "genetic" style of research also are clearly present in Mendel's work, however, as is suggested by historiographers who seek to place Mendel back in his nineteenth-century context rather than read him, as geneticists so easily do, as offering the first modern genetic theory of factor transmission.[20] My description of Mendel's research as following a developmental process is aimed to support, at the level of research styles, the broad view of historians that biologists in the second half of the nineteenth century sought a unified understanding of heredity, development, and evolution.[21]

I also illustrate how embryologists who tracked cell lineages in development, such as C. O. Whitman, E. B. Wilson, and E. G. Conklin, adopted representational styles that became increasingly abstract and eventually led to the emergence of the theoretical causal logic of the new, genetic style of explanations. In other words, the embryological origins of the gene theory can be detected in representational strategies and empirical methods

as well as in the problem agendas, theories, and scientific pedigrees of embryologists. Since these strategies and methods were integral to embryological work, not only is the gene theory embryological in origin but genetic practice is "embryological" in origin as well.[22]

I argue, furthermore, that genetics still is "embryological" insofar as genetic research styles do not and cannot ignore or black-box embryological phenomena, although it has become standard to describe genetics as ignoring development in its abstract mapping of genotype to phenotype.[23] That is, at the level of research styles for tracking processes, the split between genetics and embryology is a matter of what is represented in the foreground versus the background of attention. The split cannot be manifested in a commitment to study one process to the exclusion of the other because heredity and development are only aspects of a single causal process. Studying one is ipso facto studying the other, just as studying cooking is ipso facto studying chemistry.

Genetics backgrounds embryological interests and problems in its methods and representational strategies for the sake of foregrounding problems and interests that are now recognized as genetic rather than embryological. But it does not follow from this that the embryological *process* is backgrounded by genetic *methods*. Thus, embryological concerns fill Mendel's many pages on how to prepare material for hybridization experiments. However, the foreground/background distinction is something recognizable only in hindsight, in the light of a *subsequently* preferred theoretical perspective or historical narrative that represents processes in terms of foregrounded problems. Moreover, as a consequence of the feedback that representations provide in the conduct of scientific work, it has become difficult to see that the phenomena, the methods, and the representations which appear throughout the history of genetic and embryological research are entangled, even though our focused attention makes them appear to be cleanly separated. The theoretical abstraction of heredity from development in modern scientific thought cannot provide a framework for understanding the history of heredity/development nor, to the extent that similar goals and strategies of unification or intersection are in play in current evo-devo research, can it provide a framework for understanding its scientific future. It was previously argued that modern distinctions (such as genotype/phenotype) are of little help in understanding the history or philosophy of the abstractions that led to them.[24]

Following a process scientifically requires a large measure of self-control and self-discipline. One aim of scientific representation is to guide

a viewer's or reader's attention in ways corresponding to the discipline required of the researcher. If representations play dual roles of reporting scientific results to outside parties and as "working objects" at the laboratory bench or field site, then attention guided by particular sorts of representations can affect the ways in which commitments to follow processes are honored and understood.[25] The contexts of intervention and representation, like the contexts of discovery and justification they replace, cannot be separated, even for analytical purposes, if representations guide marking practices, and marking interventions are the basis of representations of processes followed.

Mendel as a Developmentalist

Mendel's achievement can be correctly interpreted as a theory of development as well as a foundation of the modern genetic theory and methodology of heredity.[26] I will argue that this was Mendel's intent and not merely the fancy of a revisionist historian or philosopher in order to illustrate three points. First, Mendel's project aimed to follow a biological process along the general lines described above. Second, Mendel considered this process to be developmental, and accordingly expressed his goal as pursuit of a theoretical understanding of a key aspect of development. Third, the representational strategies that Mendel devised as working tools to keep track of his process-following work and to communicate his theory led him to formulate several distinct notational conventions in his *Experiments*. These had the effect of focusing attention (foregrounding) on what we now take to be factor transmission and defocusing attention to the developmental aspects of the process, backgrounding them as a methodology for manipulating plants in pursuit of laws of transmission rather than as the target of theoretical investigation.[27]

My argument is not that we should disregard readings of Mendel as a (proto)geneticist in favor of some more "accurate" developmentalist reading of his work. My goal is instead to try to understand how the particularities of Mendel's experimental, theoretical, and representational practices contributed to his work's incorporation into a genetic conception of the process he was following rather than into the inclusive developmental one that I believe directed his concerns.

These points suggest that Mendel's representational strategies probably played an important role in shaping the attention of his readers, scientific followers, and historical interpreters to following the developmental process that interested Mendel. As a result, we no longer clearly see in his

writings that (1) Mendel's laws (of hereditary transmission) are not Mendel's theory (of the development of hybrids), and (2) both heredity and development are integral aspects of one process, each of which must be attended to in order to track it.

What distinguishes foreground from background in Mendel's science, as well as in subsequent interpretations, is the direction of the reader's attention. The aspect foregrounded by Mendelians such as Correns and Bateson—hereditary transmission of factors in development—is represented in laws of transformation that describe the characters which Mendelians followed through experimentally generated processes. Mendelian characters are marks, in the dual sense discussed above, that Mendel noted and attended to as he followed and manipulated heredity/development. The aspect of Mendel's work backgrounded by geneticists—that there are two kinds of developmental constancy of characters which pass through the hybrid offspring—is represented in Mendel's statement of theory that leads to his laws and in statements describing the experimental practices necessary to systematically construct artificial processes of hybridization and development that can be followed. For geneticists, what Mendel calls his *theory* is merely a developmental means to lawful genetic ends, while for the nineteenth-century unifier, the laws only codify and support the developmental theory.

That Mendel's project aimed to follow a process is plain from the opening of his *Experiments*, Mendel notes on the first page that the observers who preceded him—Kölreuter, Gärtner, Herbert, Lecoq, and Wichura—pursued experiments to "follow up [in] the developments of the hybrids in their progeny" the "striking regularity with which the same hybrid forms always reappeared whenever fertilisation took place between the same species."[28] That is, the line of work to which Mendel contributed is that of following the developmental process of hybrids into the progeny. Mendel's achievement was to recognize that the statistical distribution of offspring of particular kinds can reveal aspects of the developmental processes occurring in their hybrid parents. This achievement stands regardless of whether one reads the impact of his results as bearing on the old problem of species stability, on new problems of hereditary transmission, or on the lawlikeness of hybrid development. The properties of interest throughout Mendel's work are kinds of developmental constancy of characters.

As Olby and Sapp have noted, the concerns of these hybridists were neither those of a modern geneticist nor exactly those of Mendel himself. Mendel's work has accordingly been put to a variety of rhetorical pur-

poses.[29] Many of the hybridists' experiments, for example, were conducted to explore the possibility of a direct action of foreign pollen on characters such as seed, pod, and fruit color. Indeed, when Gärtner hybridized plants to explore this question, he did not grow the second generation from the hybrid seeds because this would have been irrelevant to the problem of the action of pollen on the seeds of the hybrids themselves.[30] Mendel's work, in contrast, focuses squarely on the problem of finding a "generally applicable law governing the formation and development of hybrids."[31] Following up the development of hybrids in their progeny is precisely a problem of tracking the consequences of the developmental process that took place in their hybrid parents. It is thus a problem of following a process set in motion and artificially controlled by hybridization experiments. The process is of a kind whose inputs had been carefully explored by Mendel's predecessors, but whose outputs were studied quite differently and to different ends by Mendel.

That Mendel aimed to follow a developmental process by constructing cross-hybrid plants from purebred lines is plain in his language. Attention to Mendel's linguistic usage clarifies his theoretical goals and their relations to the laws he inferred and tested on the basis of his experimental work. Terms with the root word "inherit" occur twice in English translations of Mendel's *Experiments*.[32] There are four occurrences of words with the root "transmit." In sharp contrast, words with the root "develop" occur fifty-eight times, often many times on a single page.[33] Of these fifty-eight occurrences, eight appear in the phrase "developmental series" (*Entwicklungsreihe*), which could be understood not as a term from biology but as a mathematical term to describe the "development" of the terms forming a combination series.[34]

The terms of a combination series describe different kinds of individual organisms that could appear among the progeny of a cross in terms of the combinations of kinds of factors they would receive from their parents. A + 2Aa + a and B + 2Bb + b are examples of developmental series.[35] They refer to three kinds in a progeny—A, Aa, and a—and to four (types of) individuals—A, Aa, aA, and a—that instantiate these three kinds. "AB + Ab + aB + ab + 2ABb + 2aBb + 2AaB + 2Aab + 4AaBb" is "indisputably a combination series in which the two expressions for the characters A and a, B and b are combined."[36]

The members of this series are the progeny organisms developed in subsequent generations from parents constructed in hybridization experiments. Their representation in a mathematical combination series later in *Experiments* describes a developmental series in both the mathematical

sense of a progression of terms in a combinatorial expansion and the biological sense of a progression of offspring kinds in the developmental "expansion" of a progeny bred from the hybrids. I will comment below on this character notation in contrast to Mendel's other theoretical notations for gamete forms (pollen and egg cells), fertilizations, and results of fertilization.[37]

Most important, the order of terms in the combination and developmental series reveal something of Mendel's developmentalist thinking—a point to which I will return in discussing his four notations. The developmental variety that can be experimentally generated from hybrids was of central concern to Mendel because it posed a challenge to identification of underlying unity with constancy expressible in a law. Mendel's theoretical struggle was to relate the constancy of character *form* seen in the parental types appearing among a progeny and the constancy of *behavior* in the segregating character forms of hybrids.

Even discounting the meaning of "developmental series" as mathematical rather than biological, "develop" appears an order of magnitude more times than either "inherit" or "transmit." Moreover, Mendel's first mention of the concept of a developmental series makes it clear that he saw a connection between the mathematical expression of a combination series, which mathematically describes all possible combinations of characters, and the biological process of development of offspring of each combination or kind: "In order to discover the relations in which the hybrid forms stand towards each other and also towards their progenitors," Mendel writes, "it appears to be necessary that all members of the series developed in each successive generation should be, *without exception*, subjected to observation."[38] A developmental series thus represents a mathematical series of kinds of biological processes of development.

With this awareness of the relative frequencies of term usage, we can look afresh at Mendel's expression of his developmental concerns. Mendel writes abundantly about the development of plant characters: of buds opening before being "perfectly developed," of the withering of "certain parts of an otherwise quite normally developed flower" and "defective development of the keel," of seed shape and albumin developed immediately after artificial fertilization, of pods developed early or late, of seeds damaged by insects "during their development."[39] Thus, we know that his use of *Entwicklung* cannot always or routinely be interpreted as a vague or ambiguous term meaning "unfolding" or "evolution." These developmental concerns, tucked away in the "methods" section of Mendel's *Experiments*, are crucial to control in explicit protocols if Mendel is to be able

to track the development of hybrids by means of crossing experiments. If plant parts do not develop in constant, controlled ways, no inferences can be made about the developmental process in the hybrids, through which Mendel tracks the characters, from their distribution in the progeny. That is, if development is not suitably well-behaved, character tracking will break down in the generations bred from the hybrids.

Moreover, when Mendel moves to talk about the inferences he will draw from the experimental results of generations bred from the hybrids, his developmental language does not slip into vague or metaphorical language about development: "The proportions in which the descendants of the hybrids develop and split up in the first and second generations" does not confound what we today would think of as separable processes of heredity and development. Rather, Mendel is writing about how hybrid organisms go through embryological development in such a way that developmental kinds of hybrids can be resolved, but only by tracking the characters into subsequent generations of progeny created by self-fertilization.

Mendel is clearly concerned to systematically analyze how his constructed hybrids develop, in the biological sense of the term. This of course does not imply that Mendel had any very precise embryological mechanism in mind for the development of the characters he investigated—how tall pea plants become tall, or how plants make violet-red flowers or yellow seeds. The developmental theory he espoused[40] is that constant progeny (i.e., progeny bearing parental characters) "can only be formed when the egg cells and the fertilising pollen are of like character, so that both are provided with the material for creating quite similar individuals, as is the case with the normal fertilisation of pure species."[41] But Mendel's language does signal that his interest was, as he repeatedly says it is, in the development of and from the hybrids. And it signals the ways in which his methodology of experimental hybridization was crafted to serve that goal well.

Mendel routinely refers to his theoretical goal as an understanding of the "development of hybrids," expressed in the form of a law. In the section "The Reproductive Cells of the Hybrids," Mendel lays out a hypothesis and an assumption, which I take to be his theory of the development of hybrids and which Bateson called "the essence of the Mendelian principles of heredity."[42] Mendel's theory is built on an induction from experience with hybridization: "So far as experience goes, we find it in every case confirmed that constant progeny can only be formed when the egg cells and the fertilising pollen are of like character."[43]

Mendel then goes on to formulate the hypothesis that extends his inductive generalization from hybrids of different character to hybrids of all types, and thus to offer a theoretical hypothesis to explain the development of hybrids in general:

> We must therefore regard it as certain that exactly similar factors must be at work also in the production of the constant forms in the hybrid plants. Since the various constant forms are produced in one plant, or even in one flower of a plant, the conclusion appears logical that in the ovaries of the hybrids there are formed as many sorts of egg cells, and in the anthers as many sorts of pollen cells, as there are possible constant combination forms, and that these egg and pollen cells agree in their internal composition with those of the separate forms.[44]

There can be no doubt that Mendel took this hypothesis to be his theory or that its target was to explain the development of hybrids, though there is one caveat addressed in an added assumption needed to render the theory testable (i.e., amenable to what Mendel called "experimental proof"), because he goes on to say: "In point of fact it is possible to demonstrate theoretically that this hypothesis would fully suffice to account for the development of the hybrids in the separate generations, if we might at the same time assume that the various kinds of egg and pollen cells were formed in the hybrids on the average in equal numbers."[45] A few lines later, after describing the form that these experimental proofs should take—what we now call backcross experiments—Mendel predicts the plant forms (character combinations) that must develop from the hybrids constructed, "if the above theory be correct."[46]

I claimed above that Mendel's theory is not Mendel's laws and that Mendel's theory is a theory of the development of hybrids. In exploring the relation between Mendel's theory and Mendel's laws, it is important to consider a frequently overlooked feature of scientific representations: they are often working objects, developed as bench or field tools for tracking phenomena and following processes, but subsequently pressed into service as tools for communicating results and interpretations.[47] Mendel's notation is often taken for granted as a tool for expressing his "laws" of segregation and independent assortment in hereditary transmission, while the interpretation of Mendel's theoretical goals remains controversial.[48] Mendel's notation looks antiquated to modern eyes because he represented kinds of characters—A, Aa, and a—rather than factor combinations or genotypes—AA, Aa, and aa—to express developmental and combination series.[49] Many historically sensitive expositions present Mendel's work in

terms of a modern, un-Mendel-like genotype notation.[50] Mendel's own collection of notations tells an important story about his theoretical goals, gives clues for recognizing the developmental target of his explanatory laws of heredity, and, most important, reflects his shifting expository concerns in terms of what each notation foregrounds or backgrounds.

A change of notation within *Experiments* reflects a subtle shift of Mendel's attention from tracking processes of fertilization, hybridization, and development to explaining the development of hybrids in terms of the fertilization processes created by controlled breeding experiments. Mendel's first notation, "character development notation," foregrounded the problem agenda, methods, and empirical results that led to his explanation of the development of hybrids. The three subsequent notations highlight the inferred pathways of character transmission in the fertilization process that explain the patterns observed *while following the process of character development* in the hybrids. Once these germ cell, fertilization, and product-of-fertilization notations (collectively character-transmission-in-fertilization notation) are adopted and notational equivalence to the character development notation is established, it becomes feasible to formulate and attend to problems of character transmission as part of a new kind of theoretical enterprise of heredity research without speculating on the precise mechanisms and detailed behavior of development in hybrids.[51] In other words, the shift from character development to character transmission in fertilization notation facilitates a reversal of foreground and background commitments to lines of work that we recognize as alternately embryological or genetic. Instead of following developmental processes in the foreground with an implied background of characters transmitted in fertilization, the character transmission notation foregrounds patterns of transmission and backgrounds character development.

This is not to say that Mendel's work "really" concerns heredity rather than development, because his explanatory notation concerns transmission, nor to say that Mendel actually achieved this differentiation of lines of work. Rather, I claim that Mendel's notation made it easier to take for granted the developmental phenomena necessary to establish the laws "of heredity," and thus made it easier for followers to think of their work as distinct from developmental concerns. So easy, in fact, that the meaning of the character development notation has been recovered only with great analytical effort.[52]

The character development notation was motivated by Mendel's noticing the "double signification" of the dominant character in hybrids.[53] By following such characters into the second generation bred from the

hybrids, Mendel's 3:1 segregation result is resolved into a 2:1:1 ratio.[54] The 2:1:1 ratio is significant in two ways. First, if the dominant character (say, tall) is parental in character, then it is constant in the offspring and "it must pass unchanged to the whole of the offspring." But if the dominant character is hybrid in character, then it is not constant in the offspring. However, it is constant in a second sense: "it must maintain the same behaviour as in the first generation"; that is, the second generation bred from the hybrids (F_2 in modern terminology). So the first point is that the 2:1:1 ratio reveals *two kinds* of developmental constancy. One kind is constancy of character *form* of the parental characters represented by T and t in the second and third terms, or 1:1 component, of the ratio. The other kind is constancy in character *behavior* of the hybrids represented by Tt in the first term of the ratio.[55] 2:1:1 relates the equal proportions of these two kinds of character constancy—2:(1:1) or 2:2—whereas the modern genotype notation, 1:2:1, does not.

The second point is that the ratio is reported as 2:1:1 to distinguish the two kinds of *character* constancy (hybrid constancy of behavior versus parental constancy of form), not two kinds of factors (T, t) or three kinds of factor combinations (TT, Tt, tt). The dominant character, tall, thus has two forms, Tt and T, where the first denotes the constant (segregating) behavior of the hybrid form, while the second denotes the constant form of development of the parental type in the progeny of hybrids. Reporting the proportions as 2:1:1 allows the *characters* tall and short to be put into proportion at the same time that the two kinds of developmental constancy are put into proportion.

The double significance of the dominant character in a given generation is determined by tracing the process of development of hybrids forward into the progeny. The distribution of the progeny characters provides information about the developmental process (behavior) in the hybrid parent. Thus, although the tracking direction runs from ancestors to descendants, the inference and explanation of development of hybrids is from later steps to earlier ones. Moreover, the entire exercise is framed by prior knowledge from the hybridists' projects that the progeny of hybrids are variable and can be "transmuted" into parental types in virtue of the constant behavior of the hybrid characters. A similar pattern of tracking and explanation will be described for several kinds of embryological work.

At this point, Mendel introduces the developmental series A + 2Aa + a to show "the terms in the series for the progeny of the hybrids of two differentiating characters." The hybrid character appears in the middle

of the series rather than on the left side (as in his reported 2 : 1 : 1 ratio) because the point Mendel is preparing to make concerns not the distinction between the two kinds of constancy, but the mathematical behavior of the number of forms instantiating the two kinds of constancy. With continued self-fertilization the number of hybrid forms is reduced relative to those of parental forms at a ratio of 2^n-1 : 1, where n is the number of generations. The purpose of the table on p. 14 of *Experiments* is to show that the constancy of behavior of the hybrid forms leads to a constant number of hybrids in each generation, while the numbers of parental types that are constant in form increases by 2^n-1 for each parental type, each generation.[56]

Mendel's character development notation reveals the core principle of his "law of development." Although there are two kinds of developmental constancy, there can be a single law of development to describe character constancy. Tracking the two kinds of constancy of dominant characters in the developmental series A + 2Aa + a explains the observation of 3 : 1 ratios as *due to* 2 : 1 : 1 ratios.[57]

Mendel goes on to consider multiple character hybridizations in which combination series express the (mathematical) products of developmental series. Thus, a hybridization of characters with developmental series A + 2Aa + a and B + 2Bb + b yields the combination series

AB + Ab + aB + ab + 2ABb + 2aBb + 2AaB + 2Aab + 4AaBb.

Note that in this series as well, the order of terms has developmental significance. The first four terms, Mendel points out, are constant in form in both characters. The next four terms are constant in form for one character and constant in behavior for the other. The last term is constant in behavior for both characters. The mathematical behavior of combination series reflects the developmental constancy of form and behavior of characters in hybridization experiments, which bring characters together by fertilization, exhibit constancy in development, and are parceled out in the progeny generation. Thus, although combination series expressions seem to us (moderns) to focus attention on factor transmission patterns that generate the ratios explained by hereditary laws of segregation and independent assortment, the order in which terms are presented reflects a basic developmental phenomenon that Mendel discovered through experimental control of hybrid development and a commitment to represent the phenomenon as developmental.

After formulating his theory of the development of hybrids in terms of the hypothesis that constant forms in the progeny result from the

pairing of like with like, and the assumption that kinds of egg and pollen cells are formed in hybrids, on average, in equal numbers, Mendel describes a number of "experimental proofs" of the theory: confirmation of predictions of the ratios between hybrids and constant forms that must result in circumstances specified by experiments with controlled hybrid development. We need not go into details of the well-known backcross experiments, other than to observe that the predictions depend on the theoretical assumption that egg and pollen cells of all possible forms are developed in the hybrids in equal numbers. Thus the experimental proofs, like the theory itself, are developmental in character.

I mention the experimental proofs because they mark a transition between Mendel's attention to the developmental subjects leading to his theory, on the one hand, and explanation in terms of character transmission, on the other. Mendel makes the link between development and transmission the basis for claiming that the experimental proofs confirm his theory. That is, the developmental output of forms and progeny ratios from the hybrids, if the theory is true, is linked to the inputs to the hybrids via fertilization. The linkage comes in a sentence that begins with a statement about development and ends with a statement about fertilization: "the pea hybrids form egg and pollen cells which, in their constitution, represent in equal numbers all constant forms which result from the combination of characters united in fertilization."[58]

This linkage occasions a change from character development notation to a notation that foregrounds character transmission. Mendel had been following two processes in his experiments: (1) fertilization via crossing to produce hybrids and (2) development via the behavior of hybrids displaying dominant characters and their distribution in combination series among the progeny. If these processes are causally linked in a single process, then a notation designed to describe character development of hybrids ought to be formally equivalent to a notation suited to tracking characters in germ cells through fertilization. This is exactly what Mendel shows, noting that the simplest case of a developmental series for a pair of differentiating characters is "represented by the expression A+2Aa+a, in which A and a signify the forms with constant differentiating characters, and Aa the hybrid form of both." In considering the formation in development of four (kinds of) individuals from three classes of developmental constants (A, Aa, a), Mendel makes the notational link between development and fertilization by noting that the formation of the four individuals of three classes must involve "pollen and egg cells of the form A and a" taking part, "on the average equally in the fertilisation; hence each form twice,

The pollen cells A + A + a + a

The egg cells A + A + a + a

Figure 12.1
Germcell character notation.

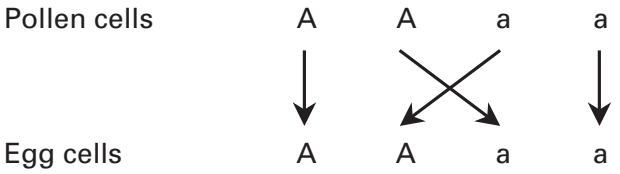


Figure 12.2
Four kinds of fertilization processes.

since four individuals are formed."[59] The formulation of the germ cell character notation follows (figure 12.1): "There participate consequently in the fertilisation. . . ."

This notation concerns the inputs to fertilization, the process which is controlled by experimental hybridizations so as to yield the development of hybrids that can be followed into the progeny generations. Mendel elaborates on the fertilization process now that he has introduced a notation suitable for describing character transmission through germ cells which follows "the law of probability" (p. 25), extending the notation to represent the four kinds of fertilization processes that yield the possible kinds of individual hybrids (figure 12.2).

One further extension of the character transmission notation clarifies the results of the fertilization process to express the developmental kinds of hybrids that result from fertilization processes. Mendel writes (see figure 12.3), "The result of the fertilisation may be made clear by putting the signs for the conjoined egg and pollen cells in the form of fractions. . . . We then have . . ."

A A a a
– + – + – + –
A a A a

Figure 12.3
Mendel's character transmission notation.

A A a a
– + – + – + – = A + 2Aa + a.
A a A a

Figure 12.4
Notational Equivalent of Mendel's character development and character transmission notations.

The preceding three figures together constitute a character-transmission-in-germ-cells notation, which is nevertheless different from the genotype notation of post-Mendelian genetics. Mendel's notation is designed to reveal the fertilization processes that bring together pollen and egg cells of like kind in which "consequently the product of their union must be constant, viz. A and a"—that is, the unions (fertilization processes) that bring about developmental constancy of form (parental characters, whether dominant or recessive). The other fertilizations (the second and third in the series) result in "a union of the two differentiating characters of the stocks, consequently the forms resulting from these fertilisations are identical with those of the hybrid from which they sprang. *There occurs accordingly a repeated hybridization*."[60] Finally, Mendel establishes the notational equivalence of his character development and character transmission notations (figure 12.4): "We may write then. . . ."

"This represents the average result of the self-fertilisation of the hybrids when two differentiating characters are united in them."[61] The rest of the section describes more complex fertilization processes in which there are many more kinds of "participators" (pollen and egg cells of specified character).

Notational equivalence is the key to Mendel's whole theoretical argument. Fertilization processes, controlled in the setup of hybridization experiments, produce hybrids with two kinds of developmental constancy. Because of their mode of expression in combination series, these developmental series can be described in a single law of development deduced from the distribution of characters in the progeny of hybrids. Thus, the characters input to germ cells in fertilization by controlled hybridization experiments can explain, via the law of development of hybrids, not only the development of hybrids but also the distribution of characters in offspring. The character development notation focused attention on the inference backward from character distribution in the progeny to the development of the hybrid parents. The character transmission notation focuses attention on the inference forward from fertilization inputs,

skipping across the development of hybrids, to the progeny distribution outputs. Thus, although the notations are formally equivalent theoretically, they foreground very different aspects of the process they both represent, and thus serve different research styles.

Perhaps I have belabored the obvious: Mendel inferred hybrid development from the distribution of characters in developmental series among the progeny. Transmission of characters, via the constitution of pollen and egg cells, explains developmental constancies of experimentally constructed hybrid parents in terms of the equivalence of their notations. But in doing so, Mendel thereby also created the possibility of using character combinations to predict character states of progeny without attention to the backward inference to the state of the hybrid parents that was required to construct his theory of development. The predictive power of character transmission notation foregrounds problems quite different from those rooted in Mendel's speculative theory of developmental processes in hybrids. That problem has become, in the hands and representations of geneticists, mere background to the discovery and use of the transmission notation suited to following characters' distributions across generations.

This exploration of Mendel's developmentalism illustrates not only the integral role of developmental thinking in the formulation of Mendel's theory and laws, but also the way in which his representational scheme linking processes of fertilization and development served a developmental goal at the same time it facilitated a shift of attention from the backward inference of hybrid development, from progeny distributions to the forward inference of character transmission.

As the founding father of genetics,[62] Mendel produced work that must count as part of genetics no matter how the field is construed. To discover that Mendel is a serious developmentalist no less than a proto-geneticist does not in any way undermine the conceptual foundation of genetics, however. Rather, it reveals a deeper connection between developmental and genetic thought than is usually admitted.[63] In the next section, I briefly discuss another nineteenth-century founding father, August Weismann, whose doctrine of germinal continuity and somatic discontinuity girds the genetic perspective but was formed in a project of unification. In subsequent sections of this chapter, I consider embryological projects organized around following processes that also suggest how representational strategies can constrain and guide attention to foreground and background in ways that complement and contrast with the Mendelian focus on character transmission.

Weismann as a Geneticist

This anachronistic description emphasizes the point that nineteenth-century pursuits of a unified understanding of heredity/development[64] are open to various interpretations. Followers who articulate lines of work can shape styles and disciplines that diverge from the work of founders, whose representations provide wide scope for variously directing attention. The phenomenon results not so much from followers seeing the founder's work "as" some particular sort of thing, like seeing the movement of the sun at sunset "as" a motion of the Earth rather than of the sun.[65] It is more a matter of "seeing in"—seeing one possibility, pattern, or process "in" a representation rather than others "in" it. The focused attention that results in "seeing in" becomes the basis for abstracting to what is and can be seen "in focus," without excluding other views from potential awareness. Shifts of focus facilitate the emergence of new theoretical commitments that may change research styles.

Complementing Mendel, the developmentalist who became a founder of modern genetics, is August Weismann, the "geneticist" who pursued a theory of heredity that could explain development.[66] Weismann's work is separated from Mendel's by twenty years of significant developments in cytology that afforded a much more sophisticated and empirically grounded developmentalism on the cellular level. Weismann's explanation of development was rejected in his lifetime, while the fundamental implications of his unified theory for heredity were incorporated into the emerging science of genetics.

As I have argued elsewhere, Weismann held a symmetrical view of development as both cause and consequence of hereditary continuity.[67] Although his methods were not quantitative or experimental, like Mendel's, Weismann sought an explanation of hereditary continuity in terms of general, integrated principles of heredity/development in accord with the latest work in cytology, including his own work on the significance of polar bodies and reduction division in meiosis, as well as the differentiation of germinal from somatic cells.

Weismann's integrated account of differentiation as the result of separation of determinants in development, on the one hand, and hereditary continuity as the consequence of germ plasm sequestration inside the cells of the developing germ line, on the other hand, can be read as both developmental and hereditarian. Embryologists in the 1890s rejected Weismann's (and Roux's) "preformationist" theory of mosaic determinants of differentiation on account of the discovery of embryonic regulation by Driesch

and others. In brief, the Roux-Weismann hypothesis became untenable, and Weismann's developmental determinism was broadly rejected.

However, those continuing to favor the nucleus as a privileged locus of developmental causation, such as E. B. Wilson, focused on germinal features of Weismann's symmetrical representations of development and on cellular processes of gametogenesis and fertilization in their own representations, breaking the symmetry between heredity and development in Weismann's theory, and making nuclear hereditary continuity the focus of theoretical attention.[68] Wilson's well-known and widely reproduced representations of Weismann's doctrine in his textbook, *The Cell in Development and Inheritance*, contributed to shifting attention toward heredity as a causal process separate from development.[69] Nuclear "monopoly" can thus be understood as foregrounding some aspects of a unified process of heredity/development in representations and backgrounding others.[70] This was a critical shift of theoretical attention by a key player whose textbook explicated and guided emerging lines of research. Wilson's representations formed the core of a new cytological perspective on the emerging discipline of genetics. The point, however, is that it was the shift of attention in Wilson's representation, not Weismann's, that served to differentiate genetics as a line of work separate from embryology.[71] While Weismann endeavored to track all the diverging cell lines of a developing body, Wilson's abstraction focused attention on the germinal cell line in a way that foregrounded a cytological interpretation of Mendelism.

Following Developmental Fate Across Cell Generations

Several kinds of embryological work focused on the problem of differentiation, the development of organized heterogeneity out of the apparent homogeneity of the fertilized egg. The contested ground of when, where, and how in development differentiation takes place is of interest here for the reflected light it sheds on research styles. Commitment to study differentiation in particular ways is reflected in the choice of what to track in embryogenesis, how to track it, and, especially, when to begin and end tracking. The question of when to track differentiates not only lines of work in embryology but also embryological research from genetic research.[72] Thus, key aspects of the split between genetics and embryology trace not to following different biological processes of heredity and development, nor to the general structure of similar inferences from tracking the same process, but to tracking commitments that lead to different research styles.[73]

Various technical means were developed for following embryos through embryogenesis, the developmental process in which zygotes or eggs become adult organisms. Later in the twentieth century, development came to mean more than normal embryogenesis, including regeneration, dedifferentiation, cancer, and other phenomena.[74] My focus is not a full description or analysis of these varied kinds of embryological work, but rather a set of comparisons with Mendel's hybridization research style.

Methods for tracking differentiation and fate determination cut across traditional categories of observation, manipulation, and experimentation, but all involve procedures for following processes by means of marking interactions. The representational tools developed at the laboratory bench in each of several lines of work facilitated not only representations of the processes tracked but also a theoretical perspective on embryological work that foregrounded problems contrasting with those characterized as transmission genetics early in the twentieth century.

The process tracked by embryologists was literally the same one followed by Mendel: the development of hybrids. Embryologists also took variable or pure-breeding material from nature or from constructed stocks, and controlled conditions of both observation and development by means of a single set of marking interventions. However, embryological hybrids had origins and tracking significance different from genetic hybrids. Embryologists did not typically mark and control the development of the organisms they studied by introducing marks prior to fertilization in experimental breeding of a whole progeny, but rather by postfertilization marking of single embryos.

Thus, the points at which embryologists began tracking typically occurred later in the heredity/development process than those Mendel tracked. Nor did their inferences have the same temporal scope as Mendel's. Marks introduced later in a process produce a shorter causal "cone" of propagating tracks, and their introduction into single embryos rather than whole progenies also narrows the cone spatially. However, embryological inferences were constrained to run along paths similar to those of genetic inferences because they concerned the same process.

In most lines of embryological work, observation was focused and controlled by marking the embryological process, either with mental marks that served the production of hybrid representations or with physical marks that hybridized the developmental system under observation. Thus, instead of aiming at a theory of the development of hybrids, the embryologists aimed at a theory of (normal) development inferred from hybridizing marks.[75] In this inverted theoretical spectrum of problems and methods,

the focus is on the path of development rather than on the hybrid character of what develops.

An important embryological problem of the late nineteenth century grew in response to Haeckel's view that differentiation of embryos into forms characteristic of particular branches of the phylogenetic tree begins with gastrulation, and that the ancestor of all life therefore resembles a gastrula.[76] Some, such as C. O. Whitman, doubted that organ differentiation is determined only at the stage where it is first observed morphologically.[77] The skeptics sought differentiation in earlier embryological stages, some by attempting to work at the cellular level to find its earliest manifestations, perhaps in the zygote or even the cytoplasm of the egg cell. These "cell lineage workers," already very familiar with the end results of development, shifted attention to early cleavage stages of blastulation.[78] They sought to identify the fate or prospective significance of cells that did not yet manifest the differentiated states of the kind of tissue or organ to be explained, whether epidermis or mesoderm, neural plate or lens, notochord or somite.

Cell lineage embryologists offered causal narratives in which the fate of a part or region becomes evident by tracking it through a sequence of stages leading to a differentiated outcome.[79] Thus, cells in embryogenesis were taken to have a double significance: a present significance at each point of observation in development and a prospective significance for future states.[80] A key representation of the results of such work came to be called a fate map, identifying cells or embryo regions in terms of fate or prospective significance rather than in terms of present significance.[81]

Although the history of this work is fascinating, I am concerned here with only one aspect: the laboratory bench representations used to track embryonic change so as to follow the process forward to differentiated outcomes.[82] Tracking work provides the basis for causal narrative accounts of prospective significance, which involves two shifts of attention: (1) from developmental outcome to some earlier stage of a central subject significant to the narrative from which to begin tracking, then (2) tracking the historical process forward in time, conceptually "back" to the future developmental outcome from which the narrative account began.[83]

At least three nonexclusive kinds of process-following in embryological work can be identified according to the kind of marking interaction used to track the process: (1) mental marking of embryos with corresponding physical marking of diagrams, (2) physical marking of embryos with artificial substances, and (3) physical marking of embryos by heterospecific tissue hybridization. These methods of following

embryological differentiation led to a variety of visual representations that foregrounded phenomena, methods, and theories we now take to be embryological and that backgrounded phenomena, methods, and theories we now take to be genetic. In the following, I will focus on a few illustrative points.

Following Embryos Back to the Future

Mendel's methodology involved (1) identification of adult characters that bred true in pure-line preparations, (2) experimental crosses to produce hybrid organisms, (3) enumeration of the hybrid progeny by character type, (4) self-fertilization to breed more generations from the hybrids, and (5) inference of the developmental state of the hybrid parents from the statistical distribution of characters among their progeny. The result was a theory and a mathematical law of the development of hybrids that describe the constancies of form and behavior of characters in development. Additionally, Mendel offered experimental proofs confirming novel predicted progeny distributions from backcrosses, which he had not used to formulate his theory and law of development.

Embryologists of the late nineteenth and early twentieth centuries engaged in tracking styles that shared important elements with Mendel's hybridization work, but with distinct goals and details of method, technique, and experimental subjects. If the tracking styles of presumptively genetic and embryological research are similar, the disciplinary split must be explained by differences located elsewhere. Nineteenth-century representations of a unified biology of heredity/development such as Mendel's and Weismann's have been read as contributions to a theory of heredity by later workers who were able to focus on those hereditary aspects of the process that had been rendered easily abstracted from developmental aspects. F. R. Lillie claimed that the problem of the relations between genetics and development was not "visualized by Darwin and by Weismann, because, for each of them, the theory of development included the theory of heredity." A few lines later, Lillie notes that "Since Weismann, physiology of development and genetics have pursued separate and independent courses."[84] Just as abstractions of heredity from development foreground the problems of an emerging genetics research style, so abstractions of development from heredity drove the emergence of an embryological research style in the twentieth century. Tracking the development of research styles is not, by itself, enough to explain them, but it is an important part of the explanatory project to document the representational

openness of nineteenth-century unifiers that facilitated the diversification of subsequent lines of research.[85]

Tracking Embryo Parts in Semi-diagrams

The descriptive cell lineage work of C. O. Whitman, E. B. Wilson, F. R. Lillie, E. G. Conklin, and others[86] presents important examples of mental marking and a mode of embryological inference aimed at interpreting the developmental significance of cells and embryonic regions.[87] In this work, scientists observed embryos developing under a microscope. A camera lucida device was fitted to the microscope in such a way that the observer could draw (trace) virtual images portraying the embryo in real time on a piece of paper adjacent to the specimen.[88] One goal of this work was to trace cell genealogy through embryogenesis as the cells divided, moved relative to each other, and became progressively obscured from view behind or within the growing mass of cells in blastulation, gastrulation, and beyond.

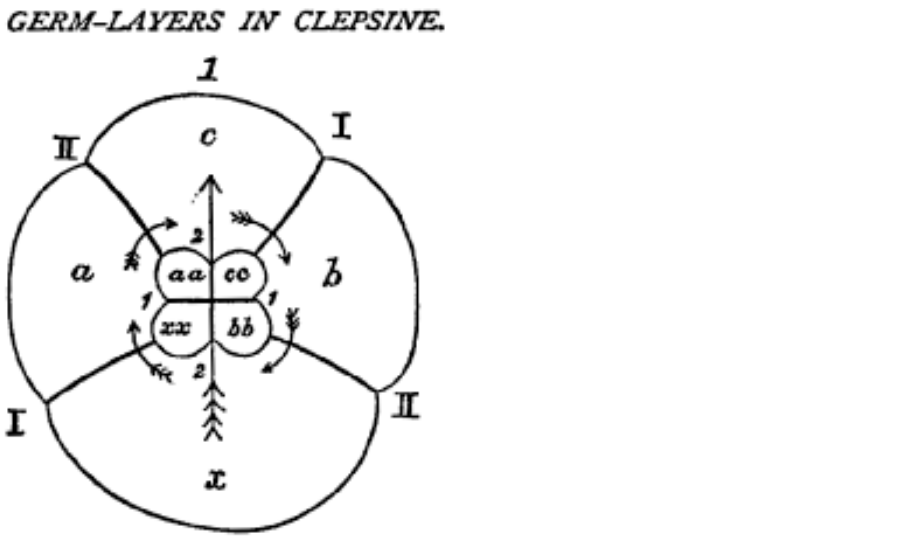
Whitman coined the term "semi-diagram" to describe the work-bench representations he produced in the course of his work with this technique. Cell outlines depicting an embryo—an embryo portrait—were traced during observation. Labels for cells and embryo regions, and arrows indicating cell movements or cell genealogy, were then superimposed on the tracing to produce a representation that is semi-diagrammatic (i.e., both pictorial and symbolic) of the process tracked by means of minute shifts of visual attention between the developing specimen and the articulated drawing.[89]

Whitman mentally marked a specimen by focusing his attention during observation on noteworthy features such as position, relative size or shape, or pigmentation, of a cell of particular interest. At the same time, he physically marked his embryo portrait in ways that turned the picture into a semi-diagram of the process he was tracking (figure 12.5). Whitman's semi-diagrams thus exhibited representational features that facilitated foregrounding of either "hereditary" (cell genealogy) or "embryological" (cell fate, differentiation) aspects.

E. B. Wilson and many other regular visitors to the Marine Biological Laboratory at Woods Hole followed in Whitman's footsteps.[90] Wilson, in his own cell lineage work, made innovative representations of cell genealogy as he traced cell lines to later stages of development (figure 12.6). In these, he brought together the representational styles of Whitman and those of Theodor Boveri in Germany, with whom Wilson had

worked.[91] Rather than depict only early embryo stages that could be fully pictured with the camera lucida technique, Wilson abstracted what he saw to produce a fully diagrammatic representation that was all symbol and no portrait. These genealogical diagrams showed only the pattern of diverging lineages, with labels to indicate some vestige of the spatial information contained in Whitman's semi-diagrams. Despite this difference, Whitman's and Wilson's techniques are similar: mentally mark the embryo in observation and physically mark a diagram to track a process of cell division leading from a determined state to a visible embryonic differentiation.

E. G. Conklin illustrates a different orientation to the problem of mentally marking embryos in order to track determined states through

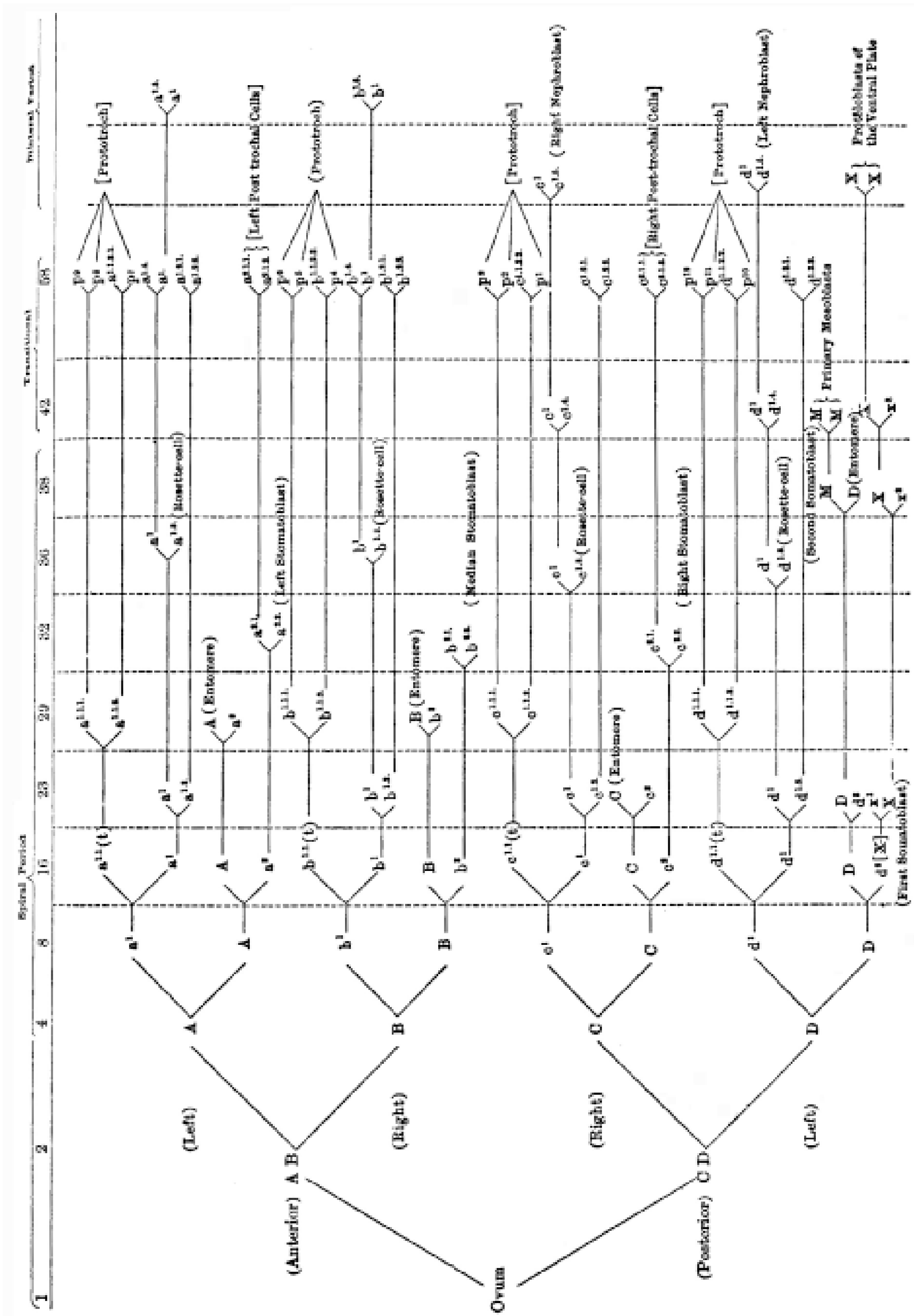


Semi-diagrammatic surface views of the egg of Clepsine in different stages of Cleavage.

Diag. 1. — The eight-cell stage, showing the relation of the embryonic axis to the first two cleavage-planes. The arrow, 2–2, shows the median plane of the embryo, and the four small arrows indicate the direction in which the four micromeres have rotated on the axis of the egg.

Figure 12.5
C. O. Whitman's "semi-diagram" (1887, diagram 1, p. 109). The camera lucida drawing of cell outlines constitutes a cell portrait, while the symbolic elements (letters and arrows) are diagrammatic. The combination of the two results in an image that is "semi-diagrammatic."

Figure 12.6 (*facing page*)
E. B. Wilson's "genealogical" cell-lineage diagram (1892, p. 382).

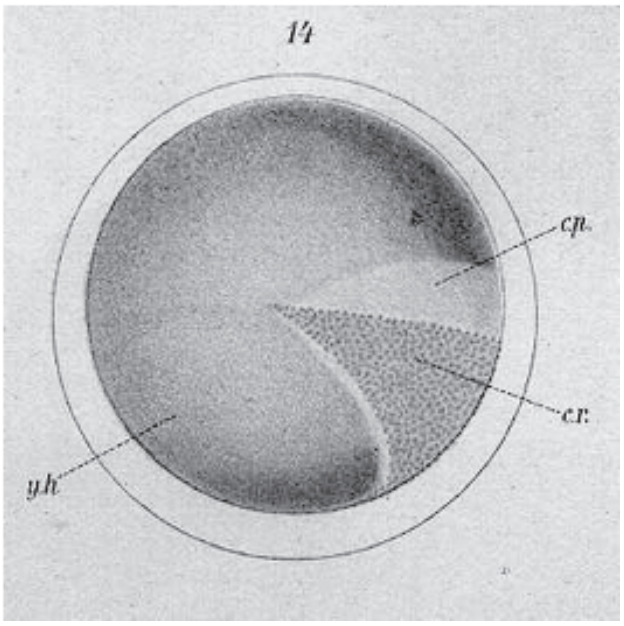

Ovum
(Anterior) A B
(Posterior) C D
(Left)
(Right)
(Right)
(Left)
Spiral Period
Transitional
(Median Stomatoblast)
(Left Stomatoblast)
(Right Stomatoblast)
(First Somatoblast)
(Second Somatoblast)
Primary Mesoblasts
[Prototroch]
(Right Nephroblast)
(Left Nephroblast)
[Left Post-trochal Cells]
[Right Post-trochal Cells]
Proteloblasts of the Ventral Plate

development.[92] Although Conklin, like other cell lineage workers, used camera lucida techniques and noteworthy observation to mentally mark cells or regions, in some cases he relied specifically on pigment markings of cells, which behaved as though the observer had introduced a persistent physical mark directly on the embryo. Other sorts of noteworthy features, such as cell position, size, or unusual shape (e.g., protruding lobes), tended to come and go during development, limiting their utility as marks. Conklin noticed that in the ascidian *Cynthia partita*, a yellow, crescent-shaped band of pigmented cells appeared at a certain point and could be followed through embryogenesis to the determination of mesodermal tissue (figure 12.7). Presence of yellow pigment in a cell at a later time meant membership in the cell lineage tracing back to the original mark.

Cell-lineage workers interpreted organ differentiation in terms of the consequences of prior determination within cell lines, as opposed to predeliniation of the actual differentiated states, at least for those species with what Conklin called "determinate cleavage" (see Conklin, 1905, p. 9). They aimed to avoid the commitments of earlier "preformationists," but at the same time focused their attention on the paths along which determined states lead to differentiated ones. As I will elaborate below, these paths of differentiation are the embryologist's version of a "hereditary" process abstracted and foregrounded from those aspects of the same process that concerned geneticists.

Here I want to make two points about research style. First, the pattern of tracking and inference parallels Mendel's work on the development of hybrids. A marking interaction is a kind of "hybridization" in the sense that it involves an intersection of two processes. In Mendel's work, an experimental cross brings together different characters and tracks them through progeny statistics. In cell-lineage work, a developing embryo and an articulating drawing are brought together by the minutely shifting, focused attention of an observing embryologist who mentally marks the distribution of cell lines and physically marks a distribution of symbols in diagrams. In both lines of work, the aim is inference about an earlier stage of the process on the basis of a distribution of progeny (organisms or cells) later on.

The second point concerns the dual role of the representations. In Mendel's demonstration of notational equivalence, the possibility of reinterpreting his work on the development of hybrid characters in terms of a factor theory of hereditary transmission was so strong that it took very careful analysis by historians to show that Mendel probably did not hold the factor theory with which he is credited.[93] Mendel's notational



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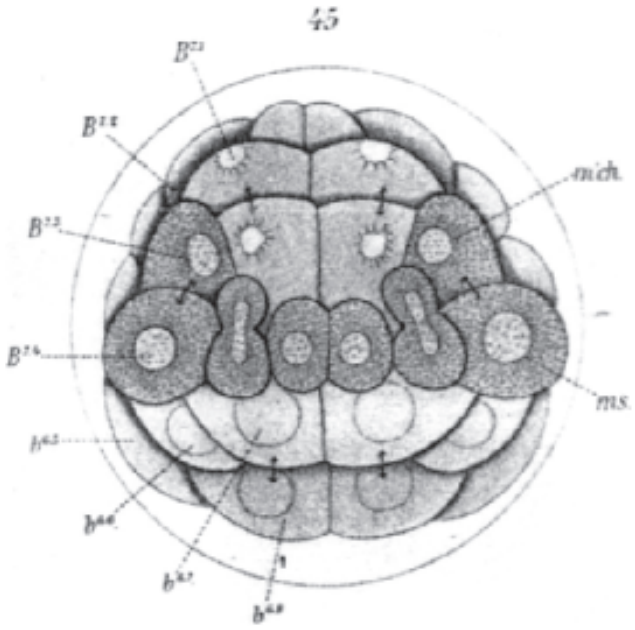

b

Figure 12.7
(a) E. G. Conklin's mental mark using yellow crescent in *Cynthia partita* (Conklin, 1905, pl. II, fig. 14). Conklin's captions for his figures 13 and 14 read: "Side views of egg, showing the formation of the crescent (cr.) from the yellow hemisphere; in all the figures the animal pole is above, the vegetal pole below. Above the yellow crescent is an area of clear protoplasm (c. p.)." In this figure, Conklin identifies a noteworthy feature that can be used as a mental mark to follow the yellow pigmented area through subsequent cell divisions. (b) A forty-four-cell stage embryo, "posterior view, showing separation of another mesenchyme cell from a muscle cell."

conventions facilitated not only his articulation of a theory of the development of hybrids but also a new, "genetic" interpretation of his developmental work by readers such as Bateson and Correns.

Mendel's character notation was designed to serve his own theoretical purposes, not necessarily those of his followers. Mendel sought to focus his attention on the independent quantitative behavior of characters in hybrids in order to support his unified, law-based theory of character constancy. The hybrids were the key because, on the one hand, they exhibited a kind of constancy (of behavior) different from that of the parental characters (constancy of form) but, on the other hand, only the progeny generated from the hybrids provided information about character development in their parents. Thus, it was important to Mendel to find a single law of constancy in order to extend the theoretical interpretation of development of hybrids to the parental characters as well.

Thus, Mendel's representations functioned both as working objects of his own theoretical investigations and as facilitators, in abstraction, of a new set of research commitments. The role of his representations in his own theoretical project served developmentalist research commitments quite different from the genetics (and developmental biology) that followed. Similar conclusions apply to cell lineage work in embryology.

First, camera lucida drawings provided semi-diagrammatic, workbench means of attending to events occurring in the embryos under study. The "virtual" quality of camera lucida images allowed minute shifts of visual attention between specimen-watching and image-making so that each mark on the drawing provided moment-to-moment feedback to visual attention *to the embryo*. Second, because the image persists after the embryo has been tracked,[94] it could be manipulated via further symbolic annotation, and new diagrams such as Wilson's genealogical diagram could be drawn to abstract features of theoretical interest from the semi-diagrams.

As I have argued elsewhere, abstraction of genealogical form from cytoembryological content through the history of cell-lineage diagrams facilitated an identification of the cell-lineage workers' findings on fate determination in embryogenesis with Weismann's doctrine of germ plasm continuity and somatoplasm discontinuity.[95] Although "Weismannism" does not accurately reflect Weismann's views any more than "Mendelism" reflects Mendel's views, it is a clear example of how the working drawings of cell-lineage workers facilitated the theoretical abstraction of Weismannism and the conceptualization of Mendelism as the foundation for a modern causal theory of heredity. Thus, the Janus faces of scientific

representations from both sides of the genetics/embryology divide facilitated the origin of genetics as a new line of work for a first generation of "embryologists" such as T. H. Morgan and W. E. Castle and as a distinct discipline for their students.[96]

Marking Embryos with Embryos

Thus far, I have focused on one line of classical descriptive cytoembryology. A similar tracking and reasoning pattern holds for manipulative experimental embryology. Walther Vogt, in a series of essays in the mid-1920s, pioneered manipulative physical marking of embryos with artificial mica chips and vital dyes.[97] (see figure 12.8.) These can be thought of as more controllable, artificial, interventionist versions of Conklin's mental-marking use of yellow-crescent pigment granules. The dyes could be accurately placed more or less at will on numerous, very small surface regions of embryos and tracked through many cell generations. This was a crucial step in extending embryological work on fate determination and differentiation to the embryos of vertebrates, which generally do not have the transparent embryonic cells of the invertebrate species studied by the descriptive cell-lineage workers.[98] While Vogt's artificial marking technique extended the research style of the descriptive cell-lineage workers, a more manipulative technique had emerged earlier that had both benefits and disadvantages compared with artificial marks.

Hans Spemann and others (e.g., Otto Mangold) engaged in transplantation experiments beginning early in the twentieth century.[99] The problem of interpreting qualitative differences of the developing cells of embryos led Spemann to his first interspecies transplant experiments in 1918 and 1919. In 1906, he had invented a technique using glass needles to conduct microsurgery on embryos.[100] He used it to transplant embryonic material between two species of newts in order to study which regions of the embryo contribute to the formation of the neural plate.

The key to the new technique's success as a marking procedure for Spemann was that one newt species, *Triton taeniatus*, has pigmented eggs, while another species, *Triton cristatus*, does not. When Spemann transplanted presumptive epidermis from *T. cristatus* into a hole cut with a glass needle into the presumptive medullary plate in *T. taeniatus* and transplanted the *taeniatus* presumptive medullary plate material into the hole made in *cristatus* presumptive epidermis, he thereby marked each embryo *in the same procedure* by which he made experimental manipulations to

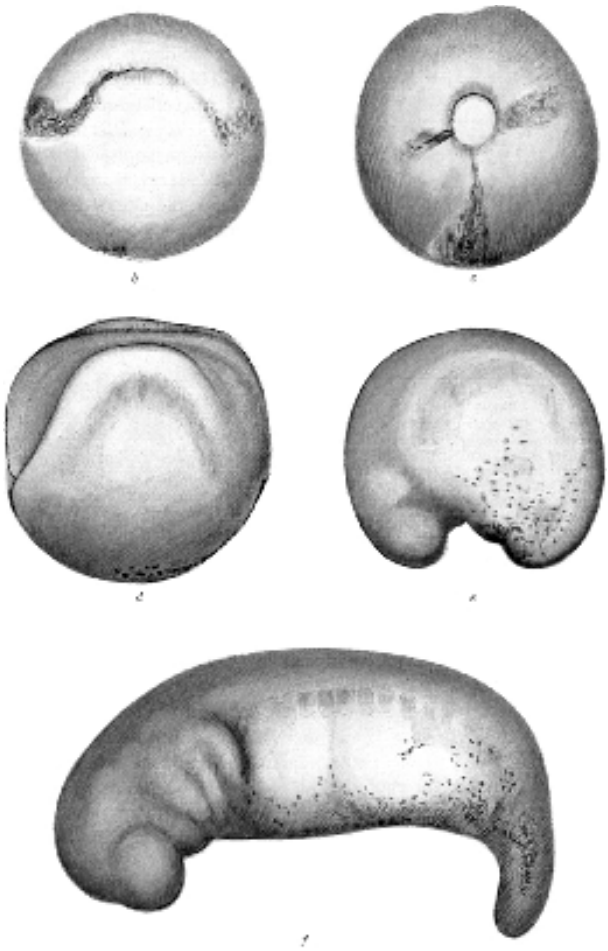

Figure 12.8
Walther Vogt (1925, fig. 14, p. 583). Vogt's physical marking technique using vital dyes. Different dyes, staining blue or red, could be traced through subsequent stages of development.

determine which kinds of presumptive tissue contributed to neural plate development. The *cristatus*-into-*taeniatus* transplant put white (unpigmented) tissue into a dark background while the complementing transplant put dark tissue into a white background (figure 12.9). The question was whether each tissue would differentiate according to its origin in epidermis or mesoderm or according to its transplanted location in the complementing kind of presumptive tissue. In these experiments, the point was not to study interspecies embryological hybrids, but only to take advantage of the marking effect of transplanted heterospecific material to explore whether regions were already determined to a particular fate or whether they were indifferent, and thus susceptible to induction.[101]

a

b

Figure 12.9
Hans Spemann and Hilde Mangold (1924, fig. 1, p. 16, and fig. 3, p. 17). Heteroplastic transplantation marking technique. Left panel: *cristatus* embryo at neurula stage with *taeniatus* implant (dark). Right panel: *taeniatus* embryo at neurula stage with *cristatus* implant (light).

Spemann's application of heterospecific transplantation in the organizer experiments of the early 1920s, conducted by his student Hilde Mangold, brought together several strands of thought and technique from the preceding decades of work.[102] The idea that the blastopore dorsal lip played a determining role in gastrulation was stimulated by Spemann's early experimental work in which he constricted the early blastula and noted that in cases where both constriction products received dorsal lip, each developed into a whole embryo, but where one received the dorsal lip and the other did not, the former developed into a small whole embryo while the latter developed into a *Baustück* of partially organized material. The idea of forming chimeric embryos grew out of experiments to explore the extent of cooperation among cells from different species.[103]

In the 1924 Spemann-Mangold paper, heterospecific transplants from *cristatus* into *taeniatus* of material from the region of the blastopore dorsal lip were conducted in order to track the progress of the lip material through gastrulation. The unpigmented *cristatus* cells appear in whole-embryo and histological sections as white cells against a background of dark cells, so structures to which the transplanted cells contribute (or wholly form) can easily be discerned. Reciprocal transplant experiments were not performed because the *cristatus* embryos rarely survived removal of the vitelline membrane during the transplant operation.[104]

The paper argues that while prior to gastrulation some regions contain cells as yet indifferent to their later fate, the dorsal lip of the blastopore is determined prior to gastrulation, so its movement inside the embryo leads it to play an inductive role. Spemann and Mangold called it an "organizer," and the region from which it was extracted, an "organization center." The transplanted dorsal lip influences its environment, but the nature of the effect depends on its precise location. Transplantation into the "normal zone of invagination" resulted in participation in normal gastrulation. Transplantation into an area of "indifferent" tissue resulted in autonomous invagination by the *cristatus* "organizer" and the development of a secondary embryo with varying degrees of differentiation and of integration with the primary embryo.[105]

Key conclusions of the paper are tentative. Although the authors are confident that the "organizer" plays an inductive role, they do not know the mechanism. They cannot distinguish with certainty between its playing the role of a mere trigger to normal gastrulation in indifferent tissue and of a determiner of the course of development subsequent to gastrulation according to a fate previously determined in the donor *cristatus* embryo. In the latter case, they write, "The organizer, by virtue of its intrinsic

developmental tendencies, would essentially continue its development along the course which it had already started and it would supplement itself from the adjacent indifferent material" (p. 38). The integration of the transplanted material, they argue, rules out its complete self-determination in the new context. Thus, the paper stands as a crucial argument for a new epigenesis. Development proceeds neither in virtue of full predelineation by inherited factors or determinants, nor with fully flexible regulation at all stages. Indeed, prior to this concluding argument, Spemann and Mangold had argued that "Definitely directed inherent developmental tendency and capacity for regulation are not mutually exclusive."[106]

Here, determined developmental states with prospective significance play the same theoretical role as characters in Mendel's work on the development of hybrids. However, the causal scope of the hybridization was restricted because transplantations were made at the blastula stage (rather than at fertilization, as in Mendel's character hybridization work) and tracking ended when gastrulae began to deteriorate as a result of complications induced by the hybridization. Spemann and Mangold created hybrid cell genealogies in their experimental transplants, so in a way they were performing the same kind of manipulation as Mendel's experimental hybridizations.

Despite the similarities, however, only in the inverted theoretical spectrum of embryology is tracking attention focused on the *path* of developmental induction in the hybridized material rather than on its developmental *state*. The developmental path and the determining role of the transplanted dorsal lip material are tracked by means of the heterogenity of hybridized embryo parts (i.e., how the white and dark materials become distributed). Tracking is used to infer the developmental state of the transplanted material (whether determined by its origin or induced to a determined state later by its new environment). However, the point of establishing the earlier state is to explain a role in the pathway to differentiation in and beyond gastrulation so as to interpret developmental constancy of the process in terms of hybrid embryos rather than to interpret hybrid characters in terms of a law of constancy of form and behavior. As Conklin had noted, determined blastomeres "are constant in their manner of origin and development" (1905, p. 95).

Importantly, embryological inferences about developmental pathways were interpreted by Spemann and Mangold in terms, if not applications, that resemble descriptions of hereditary phenomena. They wrote about "differences within the organization center that could hardly have been *transmitted* to the induced embryonic primordium by stimulation of

gastrulation alone."[107] The transmission of a determined state is no mere trigger, in other words; it requires epigenetic regulation by induction. Similar requirements were imagined for classical genes—"difference makers" transmitted from parent to offspring—to determine phenotypic differences by means of differential expression. Spemann and Mangold also wrote "that the possibility exists of a determining effect progressing from cell to cell . . . also during later developmental stages." "This conception," they continued, "of progressive determination leads of necessity back to the conception that there are points in the developing embryo from which determination emanates."[108] Their work with the experimental hybridization mark methodology goes beyond "the facts that were known earlier," which "sufficed only to establish the concept of a starting point for differentiation, but not to demonstrate the real existence of such centers. To obtain this evidence," they continued, "it is not enough to separate the region to be tested, which is believed to be such a center, from its potential field of activity. It must be brought into contact with other parts, normally foreign to it, on which it can demonstrate its capacities."[109]

These statements resemble Mendel's argument for his theory of the development of hybrids. The mental marking activity of observational, comparative embryology (like the mental marking of Mendel's hybridist predecessors) revealed deep constancies of embryological form but also overwhelming variation within phyla.[110] Only in the context of an experimental embryological hybrid, where parts are brought into interaction with parts "normally foreign to it," Spemann and Mangold argue, could the developmental capacities of a part be revealed. But unlike Mendel, Spemann and Mangold were interested in those capacities for what they reveal about the process of development, of "the main problem, i.e. the harmonious patterning subsequent to gastrulation."[111]

I do not claim that these embryological accounts of the process by which determined states are propagated "from cell to cell" constitute a theory of heredity in any current sense of the term. But they *are* elements of a theory of heredity in a sense appropriate to a turn-of-the-century unified theory of heredity/development. In order for transgeneration transmission of characters of the sort Mendel described to take place, within-generation transmission or progress of determined states must occur. Mendel's methodology did not permit cell-to-cell tracking, however, any more than Spemann's methodology allowed tracking the progeny distributions required to infer Mendelian hybrid states. Nevertheless, from both points of view, heredity and development are intertwined—in the new epigenesis envisioned in Spemann's organizer concept as much as in the new preformation envisioned in Mendel's development of hybrids.

Embryologists interested in the times and places of embryonic determination followed an inferential pattern similar to Mendel's: (1) identification of adult or other outcome states (sometimes the state of a neurula or gastrula rather than an adult); (2) marking in some way an early embryonic cell, tissue, or region; (3) tracking the marked parts through development to the outcome state; and then (4) inference of the fate or state of determination of the earlier marked part in terms of where, and how, the mark ended up in the later stage or adult. Few embryologists were interested in the sort of quantitative, mathematical laws that Mendel sought, but what is relevant to present concerns is the structure of the inferences in light of the marking interactions needed to track a process.

For both Mendel and the embryologists, work began with knowledge of an outcome state in terms of which to organize a tracking project from an early point in the process. The continuity of process tracked via marks from input to output permitted an inference of the role of the earlier stage, character, or part in determining, causing, or becoming the later stage, character, or part.

However, Mendel and the embryologists reached very different outcomes due to the particular tracking choices each made. Where Mendel used parental characters to mark development in its earliest stage (the zygote) by means of experimental hybridization, and then tracked the development of the hybrids by quantifying progeny distributions, embryologists marked early developmental stages and followed the marks continuously or continually through embryonic stages to an end stage of interest (often no farther than a gastrula or neurula). Although Mendel and the embryologists both engaged in tracking the very same process of heredity/development, where one draws attention to the relation between stages and skips over details of the process connecting them (Mendel), the other draws attention to the detailed transformations (embryologists), but within a narrowed temporal and spatial scope.

Heredity/Development Redux?

By the mid-1920s, it was clear to both geneticists and embryologists that their field of research had split, not only into separate lines of work but also into separate disciplines in distinct social worlds.[112] Those whose careers had taken them through the historical divergence, particularly leaders of the new disciplines of genetics and "physiology of development" (i.e., embryology on the way to developmental biology), had much to say about the relations between the fields as well as the prospects and desirability of "reunion" (as F. R. Lillie called it).

The present chapter serves a larger argument that the historical split between embryology and genetics in the early twentieth century—as well as the continuing conceptual difficulty of organizing genetic, developmental, and evolutionary theories into a coherent synthesis—are problems of meshing research styles and representational practices that cover the same terrain in different but intertwined ways. In my view, while discipline-forming rhetoric supported a parting of the ways between embryology and genetics in the early twentieth century, in a more fundamental sense the gene theory not only had an embryological origin, it never really left embryology at all in the broad and significant sense that includes Mendel's developmentalist project.[113]

It does not follow from the divergence of research styles and representational practices in genetics and embryology that nature is divided into separate processes of heredity and development. In this chapter, I have argued that we can detect the separation of fields in the representational practices of scientists following the one process of heredity/development. Putting heredity and development back together again can thus be thought of, in part, as a problem of conceptual reorientation—of change in theoretical perspective—to recognize that theories of heredity entail methodologies of development, and conversely. Moreover, in this chapter have I argued for a reorientation of thought about the theories: Mendel's theory was a theory of development, built on the same methodological and inferential structure of process-following as the work of embryologists. Putting Humpty-Dumpty together again may well be more a matter of instigating realignment of perspectives than of transferring tools or even problems between separated fields.[114]

There is a familiar joke about Thomas Hunt Morgan, winner of the Nobel prize for the theory of the gene in 1933, who began his career as a descriptive embryologist working on the phylogeny of sea spiders. Early in his career, Morgan turned to transmission genetics in *Drosophila*, but at the end of his career wrote a book titled *Embryology and Genetics*.[115] The joke is that the only synthesis Morgan achieved between embryology and genetics was the "and" in the book's title. Underlying the joke, and belying insiders' narratives, is the fact that Morgan persisted throughout his career in his belief that development and heredity were one subject, however asymmetrical his practical pronouncements might have been. In the year of his discovery of a white-eyed fruit fly and the beginnings of his acceptance of a gene theory of *both* hereditary transmission and trait development, Morgan wrote: "We have come to look upon the problem of heredity as identical with the problem of development."[116] His opposition

to the Mendelian theory of character transmission was not that it mixed up hereditary transmission with developmental realization of hereditary potentials, but that it got the relation between them *wrong*.

In his 1926 Sedgwick Lecture (the same year he published *Experimental Embryology*), Morgan made it clear that he was *not* arguing that development was merely a subject to be ignored by transmission genetics for practical, pragmatic reasons. Rather, he urged that careless claims by *geneticists*, which gave the impression that genetics could explain everything about development, were just as lamentable as the belief by some embryologists that geneticists must be stupid to think their work could have a bearing on the important problems of development. His distinction of heredity as a phenomenon of (mainly nuclear) transmission, and development as a phenomenon of cytoplasmic change, acknowledges the divergent styles and methods of genetics and embryology; it does *not* entail a radical Weismannist separation of *causes* of transmission and expression, however much we might read it that way today.

Indeed, Morgan was a radical defender of the role of the cytoplasm. His purpose in 1926 was to clarify and negotiate shared understanding and cooperation among diverging specialties—a task of unification, not segregation. Geneticists, he argued, were working on a different aspect of the problem than embryologists were, not attempting to explain the phenomena of development genetically. He wrote:

> There has been some criticism of the theory that the genes are the exclusive factor in heredity, on the grounds that the cytoplasm can not be ignored in any complete theory of heredity. There is no need, I think, for misapprehension on this score. The confusion that is met with sometimes in the literature has resulted from a failure to keep apart the phenomenon of heredity, that deals with the transmission of hereditary units, and the phenomenon of embryonic development that takes place almost exclusively by changes in the cytoplasm.[117]

Morgan's separation of *phenomena* can be read either as a separation of fields and styles of research or as a proclamation of a separation in nature. To speak of "the phenomenon of heredity" as dealing with "the transmission of hereditary units" is to speak of the research commitments of genetics to follow transmission processes rather than cytoplasmic changes. And his suggestion, in the same paper, that embryological work must control genetic variability, or else the production of developmental variation (i.e., variation in the causal scope of embryological tracking work) by experimental control of environment will be confounded with

genetic variation (i.e., variation in the tracking scope of genetic work), puts genetics in the cooperative service of embryology, not the other way around:

> It has long been known that the environment is one of the causes of variability in embryological development, even within the range of changes that are normal. It had not been so well appreciated, until genetics made the situation clear, that genetic elements may produce effects that superficially at least are often indistinguishable from those produced by the environment. Here, then, are two variables producing like results. Now, the most promising lead that we have at the present time *in the study of the development of the living organism* is to vary the environmental conditions—especially the temperature—in order to get data as to the nature of the processes that are taking place. Unless the other variable—the genetic constitution—is under control it is hopeless to try to get reliable data.[118]

Finally, the infamous joke book of 1934, *Embryology and Genetics*, formulates what Jan Sapp has called the "paradox of development": that genes must explain development if the theory of the gene is true, but how can they, since every cell of a differentiated multicellular body contains all the same genes?[119] Morgan stated the paradox this way: "At first sight it may seem paradoxical that a guinea pig that can develop areas of black hair should have white areas of hair if, as is the case, the cells of both areas carry all the genes."[120]

The point to notice is that this is a "paradox" about development that is to be faced by *geneticists*. It it a challenge to geneticists to understand development in order to put their genetic house in order, not a reductionist's hubris trying to show that problems of development are genetic problems. Indeed, Morgan's preferred view of the matter was that "The initial differences in the protoplasmic regions may be supposed to affect the activity of the genes. The genes will then in turn affect the protoplasm, which will start a new series of reciprocal reactions" (p. 134). This is to say that the problems of development will be solved not by looking to the genes, but to their activation by *protoplasm*.

Moreover, the critical commentaries of many prominent geneticists and embryologists throughout the period of the split (1910–1930), the rise to public prominence of genetics (1915–1930s), and the emergence of molecular biology (1940s–1970s) all show continuing concern to hold the problems of development and genetics together, despite divergent styles, concepts, theories, methods, and institutions. Thus, I favor mining genet-

ics for insights, not in support of the reduction of development to developmental genetics but for the heuristic production of a unified perspective which recognizes that genetics entails an idealized and abstracted account of development and development entails an idealized and abstract account of heredity.[121] Rather than dismissing classical genetics as merely false in its black-boxing of development, and classical embryology as backwater in its ignoring of genes, I propose that we rethink classical genetics as a false model that may provide heuristic means to a truer theory of development.[122]

Conclusion: Following Science in the Limelight

The argument of this chapter is historiographic as well as philosophical: there is a temptation to confuse the divergence of research styles in separating scientific social worlds with a historical progression of fields or lines of work that take the scientific limelight in turn. It is a reflection of the times that the historiography of twentieth-century biology has so frequently pursued "success narratives"—accounts of torch-passings from successful field to successful field as one "star" problem, method, model organism, theory, scientist, school of thought, line of work, or field takes the limelight from another. It is no doubt also a reflection of the times that the same historiography has taken the (rapid or retarded) rate of scientific progress as a primary explanatory goal.

These features are probably due in part to the uses to which scientists have put their own insider histories, and these have informed wider historical investigation. Standard histories of the origins of genetics, for example, "have explored the complex relations of genetics to embryology primarily in order to illuminate the emergence of the gene theory and genetics."[123] Fields in decline or "a period of depression," as the eminent embryologist Ross Harrison described his field in 1925, are ignored by such narratives during their low points with all the embarrassment felt in relation to a sick relative, until they finally die or rise again, as Harrison thought might have been happening in the "gold rush" to experimental embryology a decade later.[124]

Günter Stent, writing fifty years after Harrison, echoed his concerns about another root of modern embryology when he observed that despite "highly promising beginnings, the study of developmental cell lineage went into decline after the turn of this [the 20th] century. It remained a biological backwater for the next 50 years." Stent attributed the decline of cell-lineage work to the discovery of regulative and inductive

phenomena during the "gold rush" which challenged the view that cell lineage could be a causal factor in cell differentiation.[125]

Stent's interest, as a scientist, in the revival of cell-lineage work in the 1980s was "accompanied by the introduction of analytical techniques more precise and far-reaching than those available to Whitman and other nineteenth-century pioneers."[126] Thus, attention to periods of decline tends to be limited to interest in pathologies of method and poverty of imagination as explanations for lack of success. How and why the cell-lineage style of work persisted through those fifty years of decline in the backwater, so as to make a comeback in the 1980s, is a question rarely asked by those whose historical interests center on success. As Maienschein argued, "The emergence of a program in genetics has served for scholars as a favorite example of productive scientific change, specifically of theory change, and research has focused on the apparently more productive program after the change *to* genetics."[127] If our historical question focuses instead on diversifying lines of work within segmenting social worlds, then the fate of cell-lineage work becomes a key problem in the genealogy of (one strand of) current efforts to reunify heredity and development.

Maienschein looked back to uncover the sources of this productive change in the commitments of earlier research programs in heredity/development. In this chapter, I have tried to articulate conceptual resources for changing theoretical perspectives with the hope that they will be helpful in tracing forward the continuation and development of research styles practiced throughout and following the split between embryology and genetics. Specifically, I have described ways in which the practices of fields in decline, such as descriptive embryology, may be maintained in the background, as methodological commitments, for the success of projects and problems foregrounded by rising fields such as genetics. While it may be true that the fortunes of classical genetics rose while those of descriptive embryology fell, the continued practice of scientific styles out of fashion requires historical investigation if we are to understand the emergence, problems and prospects, and historical continuity of hybrid or intersectional fields such as evo-devo at the end of the twentieth century. We need to know as much about embryology and the emergence of developmental biology from 1940 to 1980 as we do of its golden age from 1880 to 1940 in order to have anything serious to say about relations between embryology and genetics. But this is made more difficult by the hegemony of success narratives trained on the scientific limelight.

Conventional narratives of the history of biology have it that Darwinian evolutionary theory was in the limelight from the mid-nineteenth

century until the phylogeny-reconstruction craze fueled by Haeckel's biogenetic law ran into trouble. Embryology for its own sake took the torch late in the century with cell-lineage, fertilization, and experimental developmental mechanics studies. The rediscovery of Mendelism and the emergence of the chromosome theory of heredity transformed the "new preformationism" into a respectable competitor to epigenesis in the early twentieth century, so that even staunch defenders of epigenesis such as T. H. Morgan were won over to a nuclear theory of the gene.[128] The rise of genetics, with its doable problems of hereditary-factor transmission,[129] displaced descriptive embryology and its nineteenth-century goal of a unified account of heredity, development, and evolution, and even eclipsed experimental embryology for a time. Experimental approaches such as Spemann and Mangold's organizer experiment brought experimental embryology back into vogue briefly, which earlier physiological and chemical embryologies had failed to do.[130]

However, the juggernaut of molecular biology at midcentury completed the ascendancy of genetics, and with it the evolutionary synthesis of genetics and systematics, which left comparative morphology and development on the sidelines.[131] Only in the late twentieth century, with renewed attention to the reunification of evolution and development (which the skeptical embryologist Lillie had already discussed in 1927 as the problem of the "reunion" of genetics and embryology), was the hope rekindled that the severed and several concerns of evolutionary, genetic, and developmental biologists might share the limelight, spurred by the excitement of discoveries in developmental genetics and deep phylogeny reconstruction, as well as by a resurgence of interest in (and confusion of) epigenesis alongside the new molecular epigenetics.[132]

While such limelight narratives make instructive drama, they confound understanding of social processes.[133] For the sake of constructing a narrative of field succession under a single spotlight of historical attention, interactions among contemporaneous, ramifying social worlds of researchers in different lines of work are submerged and made harder to investigate as continuous, going concerns. The conventional narrative frames the problems of various lines of embryological work mainly in relation to the rise of genetics rather than in relation to each other. Whole fields, taken to be represented by a single line of work that is out of the limelight, are relegated to static background "context" or "infrastructure." They then merit scientific credit only as "materials and methods." Because of the fact that embryologists have been offstage and out of attention throughout much of the "age of genetics," it is hard to explain by means of a limelight narrative embryology's reemergence in such forms as

developmental genetics, molecular developmental biology, evo-devo, and epigenetics. While Stent's 1988 notice of renewed interest in cell-lineage work was accurate, how is this line of work's historical *availability* for renewal to be explained by a genetics-centered narrative that had no need even to mention its existence for fifty years?[134]

My concern has been to describe research styles in ways that allow for the subdivision of social worlds of scientists rather than make the "naturalistic assumption" that scientists work in different worlds because they work on separate aspects of nature. When contemporaneous relations within and among fields are interpreted in terms of tracking and representing processes, we can do a better job of following the historical processes by which fields change. Likewise, when biologists understand the entwined nature of the biological processes they follow, they can do a better job of following them through the transformations that differentiate the research interests of particular fields and lines of work.

NOTES

1. Hacking, 1983.

2. Griesemer and Wimsatt, 1989.

3. Griesemer, 2000b.

4. See, e.g., Coleman, 1965; Churchill, 1974; Allen, 1975, 1985. Compose Gilbert, 1978, 1987, 2003a; Maienschein, 1987, 1991a, 1991b. For a provocative philosophical attempt to integrate foregrounded and backgrounded theories and concepts of heredity and development in evo-devo, see Winther (2001b).

5. See Gerson, 1998.

6. On following scientists, see Latour,1987, 1999.

7. Guralnick, 2002; Love and Raff, 2003.

8. E.g., Olby, 1979, 1997; Sapp, 1990.

9. Reichenbach, 1971, p. 198.

10. According to Conklin (1905, p. 93), the concept of fate traces to W. His (1874) and his concept of organ-forming germ regions of the egg protoplasm.

11. Conklin, 1905, p. 93.

12. Salmon, 1984, 148.

13. I describe the developmental process from A to B, but of course it is also characteristic of developmental thinking to view life as completing a cycle, or full circle, to return to an original condition.

14. There has been lively philosophical debate about Reichenbach's principle, in light of Salmon's elaboration of it, as to whether its invariance condition is too strong and whether its modal character raises more philosophical problems than the concept of causality it was meant to explain (e.g., Dowe, 1992; Salmon, 1994). But whatever the Reichenbach-Salmon theory's standing, scientists do engage in the enterprise their theory describes and do track the processes they follow by means of mark transmission to gain causal understanding.

15. On noteworthy observation, see Hacking, 1983, chap. 9.

16. Quoted in Sander and Faessler, 2001, p. 9.

17. See Bernard, 1865; Grinnell, 1919; Brandon, 1994 on nonmanipulative experiment.

18. This is not to say that the social world of biology *was* unified, but that a certain theoretical perspective took it to be. On the segmentation of the biological sciences in the late nineteenth century, see, e.g., Nyhart, 1995.

19. A commitment is an actual expenditure of resources, not merely the intention to spend them, and thus research commitments entail trade-offs: doing things one way entails that they are not done some other way (even if they could be on a future occasion, given enough resources, or could have been on the occasion in question, but were not). The commitment to *represent* in a particular way is what I call a "theoretical perspective" (Griesemer, 2000a).

20. Olby, 1979.

21. E.g., Allen, 1975, 1986; Maienschein, 1987.

22. On embryological origins of genetics, see Gilbert, 1978, 1987, 2003a; on representational strategies, see Griesemer and Wimsatt, 1989; Griesemer, 1994. Olby, 1997, argues that while Mendel was a developmentalist, his concerns were with developmental history (*Entwicklungsgeschichte*) and the debate over transmutation of species, not with embryological development (covered by the term "evolution"). While I agree with Olby that Mendel's predecessors in hybridization studies sought a "law-following developmental process of transmutation yielding new species" (Olby, 1997, sec. 4), I think Mendel's work stands between this older concern with species transmutability and a modern "embryological" concern with the nature of development, pursued by Mendel in inferences about the development of hybrid organisms. So perhaps it would be more accurate to say that genetic practice had a developmentalist origin, acknowledging that Mendel's practice did not arise from embryological practices of the first half of the nineteenth century (e.g., Von Baer's).

23. Churchill, 1974.

24. Maienschein, 1987; Griesemer and Wimsatt, 1989; Griesemer, 2000b, 2002a.

25. Daston and Galison, 1992; see also Gannett and Griesemer, 2003.

26. Griesemer, 2000b, 2002a. See also Gilbert, 1978, 1987, 2003a; Olby, 1979, 1997; Sapp, 1990.

27. It is not my view that Mendel actually held or understood his work to be about factor transmission. I agree with Olby (1979, 1997) that Mendel analyzed characters, not factors. However, I read Mendel's several notations for describing characters to suggest representations that facilitate foregrounding the factor transmission aspect, and thus that Mendel facilitated the reading his geneticist followers gave. Thus, I am interested in the other side of Olby's coin: just as there is a danger of whig interpretation, i.e. a story of progress toward the present, of Mendel's work through twentieth-century eyes, so there is a danger of assimilating him too closely with the goals, projects, theories, and commitments of his predecessors. Watershed figures do not resemble the water on either side of the divides they mark.

28. Mendel, 1965, p. 1. All quotations are from the 1965 edition based on the Royal Horticultural Society of London translation.

29. Olby, 1979, 1997; Sapp, 1990.

30. Olby, 1966, p. 43.

31. Mendel, 1965, p. 1.

32. I searched the Mangelsdorf print edition by hand and by a pdf download of the typeset Electronic Scholarly Publishing edition. The first is the Royal Horticultural Society of London translation. The second is a revised translation by Robert Blumberg for the MendelWeb project (http://www.netspace.org./MendelWeb/), further revised for ESP (http://www.esp.org/foundations/genetics/classical/gm-65.pdf).

33. There are also nine occurrences of the term "behavior" in the context of descriptions of behavior *in* hybrids or in hybrid unions that *produce* offspring of a given kind. I construe behavior *in* a hybrid to be an expression of a developmental property or process.

34. Olby, personal communication.

35. See Mendel, 1965, pp. 17, 19, 25, 30 for evidence that "developmental series" refers to expressions of this kind.

36. Ibid., p. 17.

37. Ibid., p. 25.

38. Ibid., p. 3; italics in original.

39. Ibid., pp. 3, 7, 9, 10, 11.

40. Also espoused by Naudin; see Morgan 1932, p. 262.

41. Mendel, 1965, p. 20.

42. See Bateson's footnote 1 to ibid., p. 21.

43. Ibid., p. 20.

44. Ibid., pp. 20–21.

45. Ibid., p. 21.

46. Ibid.

47. On working objects, see Daston and Galison, 1992. On diagrams as communication tools, see Griesemer and Wimsatt, 1989.

48. Some interpretations in the recent literature include support of evolution, anti-evolution, speciation by hybridization, laws of heredity, and development; see the discussion in Olby, 1979, 1997.

49. "Genotype" is a term introduced into English by Johannsen, 1911.

50. E.g., Bowler, 1989.

51. Mendel, 1965, pp. 25–26.

52. Olby, 1977.

53. Mendel, 1965, p. 11.

54. Modern genetics reports this ratio as 1:2:1 to reflect the combinatorics of the developmental series of *genotypes*, AA+2Aa+aa. My point in emphasizing the order of terms in the developmental series of characters, A+Aa+a, is that Mendel, 1965, p. 13, is doing something developmentally interesting in reporting his result as 2:1:1.

55. T, t represent characters, while Tt represents the hybrid form of the dominant character, not a distinct character. The different notations T, Tt for the same dominant character (tall) reflect the double significance of the dominant character in the development of hybrids.

56. Mendel, 1965, p. 14. Although it would be tempting to say that Mendel simply thought of characters as determined by pairs of factors and that his developmental series for characters (e.g., A+2Aa+a), are expansions of the binomial expression for germ cell combinations $(A+a)^2$, Olby, following Heimans, has given a compelling argument that Mendel could not have endorsed such an interpretation. Mendel, according to Olby (1979, p. 62; italics in original): "could conceive of *three* contrasted characters *which can exist together in the* F1 *hybrid*, but which are mutually exclusive in the germ cells. . . . There is, therefore, no escape from the conclusion that Mendel's conception of the character pair did not lead him to the conception of mutually *exclusive pairs of factors* also."

57. Ibid., p. 15.

58. Ibid., p. 25.

59. Ibid.

60. Ibid., p. 26; italics in original.

61. Ibid.

62. Sapp, 1990.

63. Griesemer, 2002a.

64. And evolution. Weismann, for instance, argued for a form of internal selection as a developmental process, leading to his being dubbed "neo-Darwinian" by Romanes. Although Weismann's strong internal selectionist view, like his mosaic account of development, was rejected, a variant of it made a comeback in the form of "developmental selection" in evolutionary work on clonal organisms (see Buss, 1987). While this chapter focuses on relations between heredity and development, limelight narratives of the modern evolutionary synthesis in the twentieth century present a problematic view of relations of both of these fields (and processes) to evolution. Love and Raff (2003), for example, argue that synthesis historiography has distorted the history of evo-devo relations in significant ways (e.g., by ignoring evolutionary morphology). For Weismann's larger commitments to a deeply intertwined account of variation, heredity, and development, see Winther (2001a).

65. Hanson, 1958.

66. A more accurate label for Weismann would be "Vererbungist." Churchill, 1987.

67. Griesemer and Wimsatt, 1989; Griesemer, 1994; 2000a, 2000b, 2000c, 2002a; Griesemer and Churchill, 2002.

68. This is not to say that Weismann had no hand in this way of thinking. His arguments against the inheritance of acquired characteristics in light of his doctrine of germinal continuity and somatic discontinuity (particularly in regard to his public debate with Herbert Spencer), and the expanding body of research implicating the nucleus and chromosomes in heredity, certainly contributed to Wilson's (and others') shift of attention.

69. Wilson, 1896, 1900, 1925. See also Allen, 1975; Churchill, 1974; Griesemer and Wimsatt, 1989; Maienschein, 1991b.

70. Sapp, 1987.

71. Although, as Griesemer and Wimsatt (1989) argue, Boveri had already begun to formulate the separation between problems of heredity and development in his representations of chromatin diminution in ascarids, which Boveri took to *support* Weismann's theory of development.

72. Grant Yamashita (2002) formulates the problem of germ-soma temporal differentiation as "When is a germ." Guralnick (2002) discusses temporal aspects of cell-lineage work, in particular its "teleological" character, in explaining prospective significance in terms of later developmental outcomes.

73. Clearly this cannot be the whole story, and I do not intend to explain every difference between these fields in terms of tracking activity. Rather, I think that the practices and representations associated with tracking and following provide key indicators of lines of divergence, including conceptual and theoretical developments as well as differences of problem agenda and methodology.

74. See, e.g., Berrill, 1971.

75. If one takes Mendel to have been investigating the older hybridist problem of the stability of Linnean species (see Olby, 1979, 1997), then his project is even closer to that of the embryologists I discuss because, presumably, his aim would have been to use his account of the development of hybrids to make inferences about how normal development prevents species instability.

76. See, e.g., Weindling, 1991; Richards, 1992.

77. Whitman, 1878, 1887. Others working at the same time as Haeckel and Whitman also sought differentiation earlier than gastrulation, e.g., Lankester and His. See Whitman, 1878; Maienschein, 1978, 1991a; Guralnick, 2002.

78. Maienschein, 1978, 1991a, 1991b; Stent, 1988; Galperin, 1998; Guralnick, 2002.

79. Griesemer, 2002b.

80. While the embryologists identified a double temporal significance of embryonic cells—for the adult state as well as for the immediate developmental context—Mendel had identified a double temporal significance in the future potential of the dominant character—to produce tall offspring in the first generation that are constant in hybrid behavior and tall offspring in subsequent generations bred from these hybrids that are constant in form.

81. Gilbert, 2003b.

82. See Guralnick (2002) for an argument that cell lineage work declined after 1907 because there was no point continuing to document the same pattern of development at the phylum level while failing to provide adequate tools for exploring the large amounts of variation in developmental pattern at lower taxonomic levels.

83. Griesemer, 2002b; on the notion of a central subject, see Hull, 1975.

84. Lillie, 1927, p. 361.

85. For an important attempt to explain these changes as part of a larger process of the "rationalization" of research, see Gerson, 1998. Gould (1983) described a "hardening" of the modern evolutionary synthesis that reflected a "narrowing" of perspective and attention to natural selection in evolutionary theory which is similar to the narrowings that result in subsequent lines of work on genetic or embryologic aspects of heredity/development. For Gould's account of a variety of alternative perspectives that are made possible by the representational openness of early evolutionary theory, see Gould, 2002.

86. Whitman, 1878, 1887; Wilson, 1892; Lillie, 1895, 1899; Conklin, 1897, 1905. See also Maienschein, 1978, 1991a; Stent, 1988; Galperin, 1998; Guralnick, 2002.

87. Griesemer, 2002b.

88. See Hammond and Austin (1987) on the history and technology of camera lucida microscopy.

89. Whitman, 1887.

90. Wilson, 1892; see Maienschein, 1978, 1991a.

91. Maienschein, 1991b, p. 228.

92. Conklin, 1905.

93. See Olby, 1979, 1997.

94. Of course, the embryo could be fixed and sectioned and further images made, or the embryo could be turned into an image. See Sander and Faessler, 2001.

95. Griesemer and Wimsatt, 1989; Griesemer, 1994, 2000a, 2002b.

96. To take only one almost random example (i.e. within easy reach in my office), Castle's textbook, *Genetics and Eugenics* (1916; 3rd ed., 1927), displays Wilson's diagram of "Weismann's doctrine" on p. 56 in part II, "The Historical Development of Genetics." Part III, "The Essential Facts of Genetics," begins with "Mendel's Law of Heredity." This order of presentation, using Weismannism as a conceptual guide to the understanding of Mendel's work as foundational for modern biology, was common in American biology textbooks from about 1910 to 1933.

97. See, e.g., Vogt, 1925; fig. 8. For further discussion see, e.g., Sander and Faessler, 2001.

98. Brauckmann and Gilbert, 2004.

99. Willier and Oppenheimer, 1974, p. 145.

100. Hamburger, 1988, p. 20.

101. See Willier and Oppenheimer, 1974; Hamburger, 1988; and Sandler and Faessler, 2001 for further details of Spemann and Mangold's experimental techniques and the history of the organizer experiment.

102. Spemann and Mangold, 1924; Sandler and Faessler, 2001. All quotations from Spemann and Mangold are from the Hamburger translation reprinted in Willier and Oppenheimer, 1974, and in 2001 in the *International Journal of Developmental Biology* 45(1):13–38. Page references are to the 2001 reprint.

103. Sandler and Faessler, 2001, pp. 4–6.

104. Spemann and Mangold, 1924, p. 29.

105. Ibid., p. 37.

106. Ibid., p. 35.

107. Ibid.; emphasis added.

108. Ibid., pp. 35, 36.

109. Ibid., p. 37.

110. Guralnick, 2002.

111. Spemann and Mangold, 1924, p. 35.

112. Compare Morgan, 1926; Spemann, 1926; Lillie, 1927; Brachet, 1927; Conklin, 1929; Harrison, 1937.

113. Gilbert, 1978; see also Griesemer, 2000b, 2002a.

114. Cf. Love and Raff, 2003.

115. Morgan, 1934.

116. Morgan, 1910, p. 449.

117. Morgan, 1926, p. 490.

118. Ibid., p. 492; italics added.

119. Sapp, 1991.

120. Morgan, 1934, p. 134, quoted in Griesemer, 2000b, p. 271.

121. Griesemer, 2000b.

122. Wimsatt, 1987.

123. Maienschein, 1987, p. 79.

124. Harrison, 1937, p. 370.

125. Stent, 1988, p. 225.

126. Ibid., p. 226.

127. Maienschein, 1987, p. 80.

128. On the new preformationism, see Gould, 1977; on Morgan, see, e.g., Gilbert, 1978, 1987, 2003a.

129. Kohler, 1994.

130. Spemann, 1927; cf. Gilbert, 2003a.

131. Mayr and Provine, 1980.

132. Newman and Müller, 2000.

133. Kuhn, 1970.

134. Perhaps "rehabilitation" would be more apt than "renewal." If cell-lineage work fell out of favor because it was (1) descriptive in an age of experimentalism, (2) holistic and genealogical in an age of rising nuclear causal-analytic determinism (by appealing to the ancestral cell line as a cause in development), and (3) focused on comparative morphology in an age of rising formalism and quantification, then these "faults" would somehow have to be excused and explained away to justify renewed interest.

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