Romanticism and Victorianism on the Net

The Fertile Darwins: Epigenesis, Organicism, and the Problem of Inheritance

Devin Griffiths

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Abstract
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Biographical note
Devin Griffiths is Associate Professor of English at the University of Southern California. His research examines the intersection of intellectual history, scientific literature, and the digital humanities, with emphasis on nineteenth-century British literature and science. At the center of his research is the question
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“Be careful the thought-seeds you plant in the garden of your mind,
For each seed grows after its own kind.”

Funkadelic, “Good Thoughts, Bad Thoughts”

1. Is there a “Darwinian imagination”? To date, much of the work on the relation between Erasmus Darwin and his more famous grandson has been focused on their scientific theories – especially how Erasmus’s theory of evolution might have influenced the theory of natural selection. A key challenge for studying the relation between the Darwins has been the wide difference in their reputations and in the afterlives of their most precious theories. Erasmus’s imaginative and poetic speculations about evolution were ridiculed by subsequent generations. Charles, by contrast, is now often recognized as the most important naturalist of the nineteenth century – as a paragon of Victorian scientific virtues rather than an epigone of his grandfather’s fanciful conjectures. Charles would later claim defensively that his grandfather’s thinking had not had “any effect” on his own. Even in my own work, I have argued that Charles succeeded where his grandfather failed, in shaping a coherent argument for evolution rooted in the differential and contingent narratives of natural selection.

2. Even so, in asking whether there is such a thing as a “Darwinian imagination” – by which I mean a mode of speculative thought that bridges the various rhetorical, disciplinary, and historical divides between their writings – I pose the question of what their respective visions might share beyond the technical features of their specific theories of nature. In spite of his self-presentation as a sober Baconian empiricist (the qualifier “careful” is used more than thirty times in the first edition of *On the Origin of Species*) Charles Darwin’s notebooks and private papers show that, much like his grandfather, he was an extraordinarily ambitious and imaginative thinker. Privately Charles referred to these speculations as “castles in the air” – experiments in thought that attempted to frame out speculations that were often not amenable to experimental study. The hypothesis of natural selection was itself an example of such speculative thinking. It has sometimes been easy to forget, especially given the powerful support provided by the “new synthesis” of genetics and Darwinian thought in the 20th century, just how tenuous the evidence for evolution seemed to be. A key object of the history and sociology of science in the last several decades has been to recognize the complex and uncertain place of such theories in their time and amid the debates that they spawned. The success of natural selection continues to make it hard...
to see just how outré the theory seemed. And it is this outlandish ambition – recognized as the audacity of his various attempts to reimagine the natural world from the ground up – that continually brought Charles closer to his grandfather.

3. For this reason, the present essay argues that the common impulse of their imaginations is more clearly evinced by the basic presuppositions they shared about how the natural world works – what Louis Althusser termed the “spontaneous philosophies” of scientists – rather than in their developed theories. The theories of reproduction and generation produced by both Erasmus and Charles Darwin can be viewed as projections of their respective philosophical ontologies – their fundamental assumptions about the order of the natural world, its structures and operations. All writing has an ontology, but in scientific writing the ontology of nature is front and center and (to some degree of remove) is the central matter at hand. In nineteenth-century realist fiction, by way of contrast, the basic ontology of nature is not usually at stake. Science and nature writing (and here I include all the major works of both Erasmus and Charles) are centrally about a natural ontology, whether or not that ontology is brought to the fore as an object of explicit discussion.

4. The theories of reproduction furnished by Erasmus and Charles Darwin provide powerful portraits of those respective ontologies. In confronting the mechanisms of reproduction – the means by which features from the parents are transmitted, combined, and then grow exponentially into a new being through the assimilation of new matter – both Darwins were forced to articulate a basic ontology that answered key questions about the natural world: Is matter inert or vital? Where does organic organization come from? How does nonliving matter get converted into the stuff of life? In approaching these problems, the Darwins shared a basic and (to some degree) idiosyncratic belief that all life shares a common biological basis. In particular, they believed that plant and animal life not only share a common history, but share their basic mechanisms. Their commitment to a singular ontology of life is evident in all aspects of their respective careers and especially in their seemingly compulsive return to analogies drawn between plant and animal life, and between the vegetative and the human. This commitment to life’s shared basis was determinative in their theories of reproduction because it forced them to articulate those theories in a way that could identify sexual reproduction in animals – by way of the insemination of egg or womb – with the fertilization of plants by pollen. Moreover, this commitment to a shared-in-common life meant that their theories had to also address other, nonsexual forms of reproduction and growth, from reproduction by fission (simple division), and by budding (seen in plants, some monacellular organisms, and corals), to the regrowth of limbs in animals. In exploring the
sexual theories of reproduction offered by both Erasmus and Charles Darwin, it is therefore important to recognize that neither explore sexual reproduction as one generative mechanism among many, but rather, imagine a single differentiated system of assimilation and growth.

5. In studying the relation between the integrity and development of living beings, both Erasmus and Charles Darwin struggled with the connection between inherited information and structural order, between the combined material and informatic building blocks of life and the highly organized structures and behaviors that constitute the organism. Erasmus’s epigenetic theory – most clearly set out in his scientific masterwork, Zoonomia (1794) – posited the central importance of sensitive structures. Erasmus postulated that these “living filaments” interacted with their immediate environment (whether egg, womb, or floral body), and could selectively adapt, absorb, and transform that environment through absorption and the addition of material elements. In essence, Erasmus posited a drastically attenuated mechanism of sensation as the foundation of reproductive genesis and the organism’s ability to create an ordered complexity through the absorption of additional material. Moreover, he argued that the self-directed development of rudimentary sensory apparatuses ultimately produced the more complex organs of living bodies, whether plant or animal. This sensational ontology helped Darwin explain evidence of evolution toward more complex life. It also, as Dahlia Porter explains, linked Enlightenment vitalism with Linnaean taxonomy in far-reaching ways. And yet, as we will see, even as this theory emphasized a sensitive mechanism of centralized control, it opened up the developmental process to the intrusion of outside agencies – a possibility forestalled by alternative theories like preformation.

6. Charles’s theory of “pangenesis,” by contrast, completely rejected the notion of a central mechanism of organic control in favor of the relative autonomy of the body’s structures and the “elective affinities” of their material components. Set out in his 1868 study, The Variation of Animals and Plants Under Domestication, the theory of pangenesis distributed the mechanisms of inheritance and growth even more widely across the body and its environment. Charles suggested that the sex cells do not organize inheritance and reproduction, but rather, that all cells and structures of the body spin off highly structured particles or “gemmules” that, in reproduction, gather within the sexual gametes and ultimately construct new offspring. Charles envisioned the body as less an organized whole, governed by centralized control and order, than a collective of relatively autonomous cellular agents (Darwin, Variation 2:357-403).
7. As I will explain, the two theorists staked out opposite positions on a much older debate between epigenesis (championed by Aristotle) and panspermia (attributed to Democritus). Yet behind these distinctions between their theories of reproduction, I will argue, stood a more basic commitment to the autonomous and deeply relational nature of living systems and their capacity to self-assemble into larger complexes. Both Erasmus and Charles rejected a strongly programmatic nature in which God, the great designer, prescribed the features of living creatures. Both imagined organisms as relatively autonomous and self-directed, not only in their actions, but in the mechanisms of reproduction and growth. This redistribution of agency and control, in turn, was a prerequisite for their respective thinking about evolution, not only because it furnished mechanisms by which differentiation and speciation might occur, but more importantly, because it rejected out of hand the notion of a fixed ontology, secured by a first cause, which would hold the development of living creatures within proscribed limits. Consequently, while an insistence on the relative autonomy of the organism would seem to reinforce our sense of its organic integrity, that is, our sense that any creature is a self-enclosed integration of both structure and function, we will see that both Erasmus and Charles understood that integrity as a more tenuous assemblage built up out the dynamic interaction and transformation of organic parts via interaction with the wider natural world. As Amanda Jo Goldstein describes it, such thinking encourages a “turn from self-sufficient integrity toward a proto-ecological notion of contingency and interrelation” (Goldstein, 74). This shared commitment to a more open, more flexible ontology established the Darwinian environment in which their imaginative theories might flourish. Ultimately, this shared commitment to a more open ontology provides a model for relationships and interactions – in time and across history – that exchanges a linear model of causal influence for a more collaborative conception of engagement, whether between people or the things that constitute them.

I. Preformation, Epigenesis, and the Problem of Organic Causation

8. Though I will ultimately argue for the open-ended and relational nature of Erasmus Darwin’s vision of nature, in its broad strokes his theory of reproduction, as developed in The Botanic Garden and Zoonomia, was programmatic and deeply androcentric (a position radically revised in later works). Arguing that a sensitive filament constituted the basis of the male contribution to reproduction, Erasmus posited that this filament decisively selects, absorbs, and accretes the
nutrition furnished by the womb, egg, or floral body, metabolically determining the ultimate development and structural features of the mature organism (Darwin, *Zoonomia*, 1794, 1:480–94). Theorizing that the living filament that seeds new life originated as an extension of the nervous system of the male parent, Erasmus Darwin argued that its specific configuration in higher organisms was partly determined by the mental state of the male partner at coitus, even going so far as to argue that it was this imaginative state (whether focused on the other partner, the self, or absent persons) that determined the sex of the child (1:514-9). In this way, Erasmus Darwin’s reproductive theory recast procreation as an act of sexualized Romantic creation: the imaginative imposition of masculine form on feminine substance.

9. Yet this notion of masculine form is radically undermined in *Zoonomia* when it is placed within his wider framework for thinking about the ontology of nature. And a consideration of the longer history of thinking about ontogeny – the origin and development or organic being – can help explain why. In arguing for epigenesis, Erasmus Darwin was intervening in a debate that was truly ancient. Aristotle’s *On the Generation of Animals* (referenced in *Zoonomia*) had extensively explored these two opposed schools of thought. The first, the atomist school led by Democritus, argued for “panspermia” – the theory that young are generated by spermatic elements derived from all parts *(pan)* of the bodies of *both* parents. The alternative, advanced by Aristotle himself, held that the foetus developed epigenetically – that is, in reaction to the stimulation of the male spermatic material from “without” *(epi)*. If, in the former view, offspring are formed by a union of elements derived from each parent in roughly equal measure, in the latter view, the female uterine material provided a kind of formless matter given shape and structure by the formative principle furnished by the male.

10. H. De Ley has given an excellent summary of this debate (148-50). Aristotle resolved the problem of sexual differentiation by insisting on a difference between *potential* and *actual* form. In Aristotle’s view, the feminine tissue furnishes all of the ingredients for either male or female development *in potentia*, but these are selected and actualize by the formative principle furnished by the male partner. Like Erasmus Darwin’s later theory, it was the interplay between the feminine matter and the actualizing principle of the male spermatic tissue that determined all features of the young, including sex. The other and equally important difference between the Democritean and Aristotelian schools was in their approach to causality. If, in the Democritean system, causality is distributed, the product of a more or less contingent collaboration between different material factors, Aristotle’s theory of generation injected a strong notion of causal
inference, in which the male element serves as the controlling or formal cause that gives shape to the offspring through the mediating or material cause of the feminine tissue. In the former theory, agency is distributed; in the latter it is local and univocal.

11. This configuration was fundamentally reset in the Enlightenment, as new microscopic technologies made possible a series of experimental observations by William Harvey, Antonie van Leeuwenhoek, Nicolaas Hartsoeker, Nicolas Malebranche, and Charles Bonnet. In studying the structure of the sperm and egg cells, these new “preformationists” became convinced that adults are an expansion of structures already contained, prepackaged and entire, in the germ line of the parent – though they disagreed whether it was the egg cell or the sperm that contained future generations. This new theory of preformation retooled causality by implying that all present life was predesigned and, in some sense, built into the original parents of any given species, however many generations ago. Preformation underlined a notion of the “first cause” consonant with Christian theology: whereas Aristotelian epigenesis located causality in the interaction between male and female reproductive elements, the new preformationists made cause both internal and anterior to the embryo.

12. Against this background, Erasmus Darwin presents an unsuccessful and, for that reason, fascinating attempt to return the problem of agency to an Aristotelian framework that saw causation as eminent within the world rather than ultimate. At the same time that Erasmus Darwin held that “the productions of nature are governed by general laws” (Zoonomia 1:485), his careful consideration of the implications of embryogenesis often pointed toward a notion of causality and agency that was far more distributed, even Democritean. For one, Erasmus held, with Linnaeus, that the hybridization of distinct species might have often led to successful new species, not just sterile “mules” (1:499, 514). Such full hybridization of species implied that the female parent must have significant influence over the structure of the offspring, an argument Erasmus implies in his critique of preformation (1:497).

13. Such considerations, Erasmus admitted, implied that the feminine “nutriment” was not simple matter but must consist of “ultimate particles” which formatively impact the development of the offspring. In later stages, Erasmus reasoned, the nervous system, through the action of a fully-formed digestive system, would be able to assert more control over its development, breaking down those “ultimate particles” into simpler units that could then be subsequently and selectively assimilated. But by that point, as shown by the production of hybrid species, the influence of the mother is equally determinative, scrambling Aristotle’s strict distinction between formal cause
and passive matter. If feminine “particles” help to determine the development and behavior of offspring, this means that the mother also contributes formally to the organization and action of the offspring. Far from passive matter, the uterus, egg, or floral body contributes important structural information to the young. Hence the androcentric impulse of generation fails to overwrite a more equitable contribution of both sexual partners to the formation of young. Such determinative and vital interactions are a general feature of matter, especially organic matter. 

*Zoonomia* implies a basic ontology of life that the male filament is not able to overwrite, an ontology that admits the spontaneous volition of organic matter (whether derived from the female or male) to associate, interact, and assemble into more complex units. It is foundational to the “vitalist poetics” that, in Catherine Packham’s analysis, underwrites his poetic and scientific writings (Packham, Chapter 5).

14. This tension between spermatic form and a more general and vital principle of assembly plays out at multiple points in *Zoonomia*, and is clearly registered wherever the problematic of causal agency inflects the syntax of his descriptions. Note the slippery agency in his extended later description of the relation between digestion and the apposition of material from the mother:

> In this process we must attend not only to the action of the living filament which receives a nutritive particle to its bosom, but also to the kind of particle, with respect to form, or size, or colour, or hardness, and secretion. Now as the first filament or entity cannot be furnished with the preparative organs above mentioned, the nutritive particles, which are at first to be received by it, are prepared by the mother; and deposited in the ovum ready for its reception. These nutritive particles must be supposed to differ in some respects, when thus prepared by different animals. They may differ in size, solidity, colour, and form; and yet may be sufficiently congenial to the living filament, to which they are applied, as to excite its activity by their stimulus, and its animal appetency to receive them, and to combine them with itself into organization. (1.512-3)

The passive constructions are pointedly ambiguous: if the incomplete “first filament” cannot “be furnished” with digestive organs at the outset, the “nutritive particles” are, in fact successfully “prepared by the mother” and “deposited.” Moreover, those particles then “excite” the “activity” of the filament, and even more tortuously, excite “its animal appetency … to combine them with itself into organization.” So: the feminine particles *excite* the male filament *to combine with* the particles into organization. This syntactic construction completely deranges the Aristotelian
model, in which the male formative principle stimulates the potential form of the female into action. Here the potentiality of the male filament is activated and given determinative direction by the female elements and the structural (read formal) information they encode.

15. The distributive syntax creates an environment of shared agency, an environment that completely upends the connotative distinctions between actively formative male filament and receptive feminine elements, and cultivates a far more relational and distributed field of interaction. In such passages, Erasmus Darwin’s theory of reproduction looks less like a theory of epigenesis than an early theorization of pangeneses. It implies an ontology in which the organism is not the product of a localized formative impulse, but rather, consists in the formative and contingent interaction of internal and exterior elements—an emergent ecology of interacting agents rather than a formal unity.

16. My point is that such moments mark the devolution of the sexual logic that Erasmus Darwin employed in his attempt to revive Aristotelian formalism as a model for the development of offspring. Such passages distribute agency and control, the distinction between formal impulse and matter, into a much wider, more sociable, and more distributed network of interaction, relation, and assembly. This is really of a piece with the cosmogony Erasmus laid out in his earlier writings. These two trains of thought reflect two basic and deeply divided impulses in Erasmus Darwin’s own thinking, a kind of formative tension between Aristotelian and Democritean schools. As I explain elsewhere, his *Phytologia* (1800) and *Temple of Nature* (1803) would eventually cashier the Aristotelian theory of epigenesis completely in favor of a model of elective affinity that offered a more distributed understanding of material, organic, and erotic agency.

In the third, “corrected” edition of *Zoonomia*, Erasmus makes the reversal indicated in *Phytologia* explicit: “I am now induced to believe, that the embryons of complicate animal and vegetable bodies are not formed from a single filament as above delivered; but that their structure commences in many parts at the same time” (Darwin, *Zoonomia*, 1801, 2:277–78). But this shift was well under way by the early 1790s, as manifest in the confrontation *Zoonomia*’s first edition stages within the ontology of nature. This more equable view of life marks his most substantive contribution to the Darwinian imagination.
II. Charles Darwin and the Theory of Pangenesis.

17. Charles Darwin was a brilliant thinker, and an assiduous reader and note-taker, but he was often careless about the original sources for his key lines of thought. As many have noted, Erasmus Darwin is barely mentioned in the first sketch of previous theories of evolution that he appended to the third UK edition of *On the Origin of Species* (1861) despite the fact that Charles had carefully studied *Zoonomia* both in college and in 1837, when first assembling evidence for this theory of natural selection. It is almost certain that Erasmus’s description of Buffon’s theories in *Zoonomia* afforded Charles his first exposure to the Democritean tradition; Buffon’s revitalization of that tradition via the self-assembly of what Erasmus termed “organic particles” seems to have had a determinative influence on Charles and his proposed mechanism of inheritance and growth, in which gemmules are thrown off from parental cells – or “organic units” (370) – and then subsequently direct the growth of progeny. When Charles showed a draft of the theory to T. H. Huxley in 1865, Huxley alerted him to the filiation between his thinking and similar speculative theories by both Buffon and Herbert Spencer.21

18. The first editions of the *Origin* taught Charles the importance of acknowledging antecedent versions of his theory, and he begins his discussion of pangenesis in *Variation* with a dutiful recounting of earlier speculations. Darwin’s discussion of Spencer’s theory is particularly instructive because (as Spencer later complained22) it does little to explain where they differ, saying that they are “fundamentally the same as mine” except for in certain passages, which he cites without further commentary.23 In such moments, Darwin bumps into a basic disagreement with Spencer – rooted in their respective ontologies of life – but he lacks the philosophical vocabulary to articulate the difference as such. Spencer consistently emphasized the grand harmony of natural (and ideally, social) systems; he argued that living systems, like the solar system itself, are characterized by a constant centripetal pull toward “state[s] of equilibrium” (Spencer, *Principles of Biology*, 1:356). Darwin, by contrast, reveled in the idiosyncratic, unusual, and disturbed.24 This basic difference in orientation meant their theories of reproduction, though formally similar, had radically opposed implications.

19. Darwin’s discussion of “reversion” – the phenomenon exhibited by offspring that manifest a spontaneous reversion to an ancestral characteristic not evident in its immediate progenitors – underlines his interest in life’s eccentric tendencies. Charles saw reversion as a key piece of evidence for his theory of pangenesis, which held that gemmules could survive dormant for
generations of descendants before finally being taken up and incorporated into the structure of young. (Hence his emphasis on reversion or “atavism” in Variation, which describes various disturbances of typical states, including also inherited diseases, as “asymmetrical deviations of structure” (2:1).) Spencer’s system relied on the notion of continuous and complete adjustment and equilibration. His committed belief that biological life was essentially continuous with Newtonian physics meant that any change to an element of a biological system induced a corresponding change to all other elements, much as the alteration of the orbit of any one planet would change the orbit of all others in its system. By contrast, reversion showed Charles that, far from a constant movement toward distributed equilibrium, inherited structural information could rest, stable and dormant, across many generations, and could manifest as sudden, almost unintelligible disruptions of development. For this reason, Charles termed it “the most wonderful of all the attributes of Inheritance” (2:372). Darwin’s complaint that there are features of Spencer’s account that are ambiguously “different” or “unintelligible” ultimately marks an ontological gulf in their assumptions about how the natural world worked (2:375 n. 29).

20. This marks the wide scope of Charles Darwin’s imaginative range. Like his grandfather, he was a deeply speculative and philosophical thinker, even if he could not acknowledge it. (As Althusser puts it, “in every scientist there sleeps a philosopher” (116).) Moreover, the evident excitement and “wonder” that Charles finds in contemplating the implications of reversion, in its testimony to the discontinuity between central biological functions of inheritance and development, shows that he was, in at least one respect, a more radical thinker than his grandfather. Erasmus, as we have seen, brushed into a vision of a far less constrained, more dynamic and potentially ungovernable nature and struggled to limit its more radical possibilities. Charles, by contrast, recognized and embraced those possibilities. At the end of his discussion of pangenesis, he explains its revolutionary implications for how we understand natural organisms, including the human body, with a series of poetic and arresting metaphors:

Inheritance must be looked at as merely a form of growth, like the self-division of a lowly-organised unicellular plant. ... Each animal and plant may be compared to a bed of mould full of seeds, most of which soon germinate, some lie for a period dormant, whilst others perish. When we hear it said that a man carries in his constitution the seeds of an inherited disease, there is much literal truth in the expression. … We cannot fathom the marvellous complexity of an organic being; but on the hypothesis here advanced this complexity is much increased. Each living creature must be looked at as
a microcosm – a little universe, formed of a host of self-propagating organisms, inconceivably minute and as numerous as the stars in heaven. (2:404)

On first glance, Charles’s ennobling vision of the organism as “a microcosm – a little universe, formed of a host of self-propagating organisms, inconceivably minute and as numerous as the stars in heaven” seems to reach for the sublime register his grandfather was famous for. Erasmus Darwin similarly imagined a deep coherence between the processes organizing microscopic, organismic, and cosmic life, but he constrained the ramifying complexity of that vision, closing out his discussion of generation with the argument that all development obeys a singular system of natural laws and a “Great First Cause” (known by tracing intermediate causes back to their source, “climbing up the links of these chains of being, till we ascend to the Great Source of all things” (1:533)). In place of a larger determining law or chain of causation, Charles underlines the unfathomable “complexity” of the organic system, and implicitly, the inscrutability of its basic principles.

Moreover, the intensely disorganizing power of Charles’s vision is driven home by the startling analogy that precedes it. In imagining each creature as “a bed of mould full of seeds” – in other words, as a plot of soil in a garden – he looks beyond the notion of the organism as a closed environment completely. Instead, Charles argues, we must see our selves as physical ecologies: assemblages of organic and inorganic components, of organic nutrients and various cell lines, of processes of interaction, gestation, and propagation that operate on widely different scales. If some “seeds” (that is, cell lines and their traits) germinate soon, some reproduce on much longer time scales, while others pass away.

This vision of pangenesis is explicitly a system defined by contingent and chance events, from the chance that brings a given seed to maturity, to the chance that has brought these seeds together in the first place. Any living form is, in some sense, an accidental collection of the seeds or “gemmules” that happened to be around at the moment of reproduction, and while some of those gemmules then interact with others and their environment more or less harmoniously to form the offspring, many don’t work at all, and many militate against its organic features. If Erasmus Darwin’s Botanic Garden was wildly innovative and brought him widespread fame, particularly in the insistent analogies it drew between plant and human life, it did not propose that we view individual organisms as botanic gardens in themselves. In his grandson’s eyes, living forms, like any natural environment (from the garden plot to the seascape) are ecologies.
23. The audacity of Charles Darwin’s ecological vision is clear when compared to two sources that had a significant influence on his thinking about the relative autonomy of organic components – Claude Bernard’s physiology and Richard Owen’s major study of embryogenesis. The garden analogy employed in the passage above, for example, seems to have been suggested directly by a passage in Bernard’s *Tissus Vivants* (1866). Bernard was a major proponent of cellular theory and advocated a focus on relative autonomy of the different tissues (or organs) within the body. In order to tease out the implications for pangenesis, Charles summarizes the latter’s account of organic autonomy: “Each organ, says Claude Bernard, has its proper life, its autonomy; it can develop and reproduce itself independently of the adjoining tissues” (2:368-9).

24. Immediately after the passage Darwin cites, Bernard provides a simile meant to drive this autonomy home: “Doubtlessly all these tissues maintain numerous relations during their life that form the basis of their collective harmony. But one might, to a certain point, compare each individual organ to a polyp [*polypier*] composed of the juxtaposition of a host of living organisms” (22). (By “polypier” Bernard meant a coral; it was understood that coral formations were actually communities of smaller unicellular organisms living on a calcium-based scaffolding.) It’s not surprising that Charles was impressed with this passage and Bernard’s coralline analogy. One of his first important scientific publications was a monograph that explained how coral reefs are formed by successive generations of coral growth and slow subsidence of the ocean floor. Yet, in exchanging Bernard’s coral for a “bed of mould” in his *Variation* Charles Darwin radically extended its implications. Whereas Bernard’s polypier consists of a group of substantially similar organisms, the bed of mould underlines an ecology in which specific life forms and cell lines might vary radically.

25. Charles Darwin’s willingness to push thinking about autonomous collectivity to its most radical, anti-organic position is evident also in his engagement with Richard Owen’s discussion of *parthenogenesis* – forms of reproduction, as in the aphids and other insects, in which subsequent generations or stages of growth exhibit strikingly different morphologies. For Owen and others, aphids were a particularly intriguing example because each sexual fertilization would produce several generations of sexually infertile but self-reproducing offspring before eventually another sexually active generation sprang up. Owen’s account is fascinating because, much like Erasmus and Charles Darwin, he emphasizes the continuity between these unusual forms of parthenogenic reproduction and other forms of generation, including sexual reproduction, fission, budding, and the formation of specialized tissues within any given host. Moreover, Owen argued that these
reproductive processes could teach us something about the collective nature of both plant and animal bodies. “The Botanist,” Owen explains, “in fact, arrived earlier than the Zoophytologist at an intimate philosophical comprehension of the nature of his composite subjects” (Owen, On Parthenogenesis, 53, emph. added). In particular, Owen singles out Johann Wolfgang von Goethe, who discovered the homologies of the vertebrate skull and had famously searched for the Urpflantze – the archetype of all plants. Acknowledging Goethe as the model for his own doctrine of archetypes, Owen explains that the more intriguing dimension of Goethe’s thought was that one might understand a plant leaf – with its attendant roots, its capacity for near self-sufficient life, and in some cases, its ability to reproduce an entire plant – as an organism itself, living in communion with other organisms as part of the larger plant (54). Though Owen seems unaware, Erasmus Darwin was a crucial contributor to Goethe’s thinking here. In the Botanic Garden and in the first edition of Zoonomia (which Goethe studied carefully), he had argued that

[V]egetable buds are analogous to animals … that the roots of vegetables resemble the lacteal system of animals; the sap-vessels in early spring, before their leaves expand, are analogous to the placental vessels of the foetus; that the leaves of land-plants resemble lungs, and those of aquatic plants the gills of fish; … that their seeds resemble the eggs of animals, and their buds and bulbs their viviparous offspring. And, lastly, that the anthers and stigmas are real animals, attached indeed to their parent tree like polypi or coral insects, but capable of spontaneous motion. (1:141-2)

Erasmus gives even fuller treatment to the composite nature of plant life in Phytologia, which Goethe seems also to have carefully digested.28 (Charles Darwin, in his long introduction to Ernst Krause’s Erasmus Darwin (1879), credits Phytologia as originating “the view, now universally adopted, that a plant consists of a ‘system of individuals’, and not merely of a multiplication of similar organs.”29)

26. An extraordinary implication threads through these analogies: that the parts of both plants and animals, “like polypi or coral insects,” might achieve an almost complete autonomy. Owen echoes this possibility (sounded by Goethe and – more quietly – Erasmus Darwin) and amplifies its range:

The question, however, is whether the tree represents such a whole, or is equivalent to one of the organized individual members; whether the leaf and the stamen may not answer rather to different individuals of the ‘body corporate,’ than to the lung or the testis of any single individual. … Our first (and the common) notion of a tree and a
coralline, as being respectively individual organisms, derives seeming support from the fact that in each species of composite plants and animals the aggregate of individuals assumes a definite or specific form, whence the terms ‘Oak,’ ‘Ash,’ and ‘Bell-coralline,’ ‘Fern-coralline’, ‘Sea-oak-coralline,’ &c. But, by parity of reasoning, the nests or ‘combs’ of certain Hymenoptera and nidamental capsules of most testaceous mollusks might be regarded as individuals. (56-7)

Owen’s proposal here bears unpacking, as he approaches the problem from two directions, the first structural, and the second temporal. First, when we think of the nature of any given collection of living creatures, living alongside each other, where do we draw the line between communal and organismic life? Why should we call a tree (which can be seen as a cluster of leaves and other structures living collectively on a large body of dead woody matter) or a coral colony (growing on a calcareous outcropping) a singular entity when we describe a cluster of mussels on a rope as a group of individuals?

27. To drive home the extraordinary complexity of this point, Owen details the first three figures of the frontispiece, which contains a startling alignment of plant, coral, and insect life as reproductive trees (respectively, illustrations 1, 2, and 3 in figure 1). As Owen explains, in all three images, the first stage of reproduction is represented by the fertilization of an egg or ovule (b) by a sperm or pollen cell (a). The first generation (d) reproduces asexually – either by gemmation or parthenogenesis – into subsequent generations (e), before ultimately producing sexually mature bodies that enable the cycle to start again. Owen’s point is that, read through an analogy drawn between different kinds of life, the distinction between generation, organism, and organ is radically unstable and perhaps even counterproductive.
Figure 1 – Frontispiece to Richard Owen’s *Parthenogenesis* (1849)

28. Despite the extraordinary power of this vision, and the way it fundamentally reimagines the basis of life beyond the organic model, Owen ultimately walks back its most radical implications for advanced living bodies, especially human bodies: “The stomach of a man if detached would not live and reproduce its kind like the polype of the Sertuliaria or the monad of the *Volvox*; nor would the lung manifest its individuality like the leaf of the Bryophyllum under similar circumstances. No!” (62-3). The strong rhetorical turn – marked by the interjection “No!” – serves
as an index to the bounds Owen wishes to circumscribe around his anti-organic thought. If one implication of parthenogenesis is that all existing living creatures can find their place within a singular tree of life, Owen insists that man does not live within it.

III. Charles Darwin and the Anti-organic thought

29. Charles Darwin, by contrast, was happy to see all of such implications through to their most radical end. Charles Lyell once wrote to Darwin about his long personal struggle to finally “go the whole Ourang” and acknowledge the actual kinship between humanity and other forms of life.\(^{30}\) For Lyell, the struggle was between his “reasoning towards transmutation” and his “sentiments and imagination,” which balked.\(^{31}\) Charles Darwin’s “reason” and his “imagination,” by contrast, were closely aligned: he often seems excited, even eager to “go the whole Ourang” — and whole polyp, the whole plant, even the whole “bed of mould.”

30. The conflict that Lyell described between reason and the sentimental imagination strikingly anticipates Althusser’s argument about the tension between scientific empiricism and ideology. But my point is not that contemporary scientists were laboring under a “spontaneous philosophy” that Darwin heroically overcame, any more than it makes sense to claim that scientific discovery is necessarily pitted against ideology. Rather, my point is that individual ideologies, conceived as distinct imaginative understandings of the world, make different natural facts possible. If all scientists are philosophers, that is because they must be. I agree with Bruno Latour’s extended arguments for the basically social nature of scientific facts: it is only under certain conditions, within idiosyncratic networks of scientific experiment and instrumentation, and within the framework of peculiar research agendas, that certain natural phenomena first become visible.\(^{32}\)

All of these encode a certain way of understanding the world, certain ontological assumptions about what is possible and what might be found. This imaginative reach makes new hypotheses and new discoveries possible.

31. Ever since groundbreaking work by Gillian Beer and George Levine, the field of science and literature has been focused on exploring how the literary imagination and its modes of writing contribute to science.\(^{33}\) In my own work, I have looked at analogies, and the relational frameworks they create, as crucial to nineteenth-century science. The present article suggests that the spontaneous ontology of each scientist is also a pervasive and important constituent of the scientific imagination.
Moreover, by insisting that such ontologies can be explored by means of the imaginative vision they support, I mean to raise the problem of the aesthetic criteria they entail, that is, the possibilities that are felt to “fit” within a given ontology, versus those that are felt to be discordant, jarring. Lyell’s distinction between what his reasoning implied and what his “imagination and sentiments” were willing to accept points to precisely this sort of aesthetic judgment, a judgment marked by his negative reaction to the theory of natural selection as it was presented over the years. This form of judgment is marked also, I would suggest, in the moments above where Claude Bernard and Richard Owen pulled back from the most radical or jarring implications of their theories, the shift in rhetorical register interjected by Owen’s “No!”

As Sianne Ngai observes, such “ugly feelings” demonstrate the role affect plays in mediating between ideology and experience, here, between “spontaneous philosophy” and empirical study (Ugly Feelings “Introduction”). Such feelings do not simply circumscribe; they help to gather in the imaginative reach and direct it toward a felt sense of the most appropriate whole. As Owen puts it, reflecting on his trees of life, “The analogy is beautifully and closely maintained throughout” (60). Ultimately, Owen’s insistence that “The stomach of a man if detached would not live and reproduce its kind … nor would the lung manifest its individuality” underlines the organic boundaries of his imagination; he is unwilling to read human life out of the framework of a robust and mature organicism, and place it into contact with less highly “organized” life. Owen, like Bernard and most of his contemporaries, was still fascinated by the closure of Romantic organicism, with its insistence (after Kant) that the unity of the organic whole and its parts evince a reciprocal relationship in which each is the means to the other’s end. For Kant and others, the primary example of organicism is the plant. Moreover, Kant insisted that the judgment of “unity” which we apply to the organism is rooted in a perception of purposiveness and applies to aesthetic perception in general. When we look to a work of art, Kant argued, our aesthetic appreciation is bound up in the work’s purposiveness – the sense that whole and part are organized around some higher cause.

This powerful notion of an intrinsic relation between organic bodies and works of art has had a long afterlife in literary criticism. As Denise Gigante observes, Coleridge secured this conception of “multëity in unity” for Anglo-American literary criticism by arguing for its importance to our apprehension of both natural bodies and literary forms (Life, 22–23). Most recent genealogies of organic form in Anglo-American criticism loosely trace the notion from the work of Kant, Goethe, and Coleridge, through Henry James’s discussions of the “art of the novel” in his preface.
to *The Tragic Muse*, and finally, through new criticism, as exemplified by Cleanth Brooks’s argument in *The Well Wrought Urn*. In *Show Me the Bone*, Gowan Dawson has recently explored the close connection between such organic thinking and nineteenth-century theories of physiological unity. Even the “large loose baggy monster” – James’s famous description of the nineteenth-century novel – marks the importance of organic wholeness in the aesthetic judgments that policed the boundaries between good and bad form in the nineteenth century.

35. Recently, Ian Duncan has argued that this aesthetic appeal to formal coherence is also one of Charles Darwin’s central rhetorical strategies in advancing the theory of natural selection. As Duncan summarizes, “Darwin’s theory emerges as a theory of form, dependent on a connoisseurial discrimination and evaluation of formal affinities and differences…. An aesthetic appeal to beauty and wonder, subsuming painful ethical considerations, becomes the primary rhetorical strategy with which Darwin makes his theory attractive to Victorian readers.”

36. A substantial portion of Charles Darwin’s wonder, in fact, marvels at the production of seeming integrity from uneven and discontinuous processes. Yet his driving impulse is to read behind the seeming integrity – to chisel away at the mortar of aesthetic experience. His writing is energized by a basic tension between the pleasurable experience of perceived integrity and the empirical discovery of discontinuity, error, and strife. In order to reformulate his grandfather’s evolutionary theories, Charles had to break away from unitary narratives (as I have previously argued). But he also had to figure out a way outside of Romantic aesthetics, insofar as the wondrous perception of nature as a seeming whole interfered with the naturalistic perception of those evolutionary occlusions, dead ends, reversions, and conflicts that served as the most important evidence of evolution.

37. Charles Darwin’s career shows an increasing skepticism toward such Romantic visions of nature, and in particular, the Romantic notion that organic bodies are purposively integrated both with their parts and within their larger environments. In one of Darwin’s most famous examples in the *Origin*, he presents a vision of an entangled bank only to emphasize how the perceived integration
of that vision – “clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth” – overlooks its basic conflicts and incoherence (489). In his earlier discussion of the “entangled bank” Darwin insisted that this perceived unity depends on a variety of chance events and conflicts:

What a struggle between the several kinds of trees must here have gone on during long centuries, each annually scattering its seeds by the thousand; what war between insect and insect—between insects, snails, and other animals with birds and beasts of prey—all striving to increase, and all feeding on each other or on the trees or their seeds and seedlings, or on the other plants which first clothed the ground and thus checked the growth of the trees! … The dependency of one organic being on another, as of a parasite on its prey, lies generally between beings remote in the scale of nature. (74-5)

The aesthetic perception of such seemingly integrated and holistic unity, he insists, belies the basic incoherence and radical divergence in the various “scales of nature” – physical, temporal, organizational – that produces what we see. Rather than serving as an index to natural integrity, aesthetic perception is perceived as an impediment to grasping the complexity of natural systems. Charles’s consistent strategy in such passages is to read through the organic integrity and disassemble it, to insist on the basic disorganization of life. His quintessentially anti-organic move regarding forms, whether we talk of species, or social customs, or the beauty of an orchid, is to show that we make a mistake in seeing these forms as distinct, integral, and coherent structures. The organism and the ecology are both unstable constellations, captured within a shifting network of supportive alliances, shifting antagonisms, and the more pervasive condition of simply being thrown together.

38. Like his grandfather, Charles Darwin shows a startling propensity to think the hardest version of his thought – to push a given insight toward its most unsettling implications. If the theory of pangenesis fundamentally upset the organicism of contemporary scientific imagination of natural forms, this seems of a piece with a basic iconoclastic impulse in his writing. I have argued for the importance of disanalogy in George Eliot’s writing as an epistemologically productive moment in which we are asked to recognize where a given model – a preconceived analogy – fails to account for what is encountered (Griffiths, *The Age of Analogy*, chap. 4). In a similar fashion I think that the Darwinian imagination – particularly in Charles’s later writing – is predicated on dis-aestheticization, or better, a negative aesthetic or “ugly feeling” that rewards the effort to look behind the perception of aesthetic unity and perceive what it obscures. What is at stake is not a
rejection of aesthetic perception, but rather, a new understanding of the relation between aesthetic unity and its critical negative moment in the perception of the complex economy of natural patterns.

39. To recognize this critical commitment is to recognize Charles Darwin as the foremost ecological thinker of the nineteenth century (and here it is important to remember that Ernst Haeckel directly credited Darwin’s *Origin* when he coined the term “ecology” in 1866 (*Generelle Morphologie der Organismen*)). On the one hand, this is hardly surprising; it is only in light of natural selection, which abandons natural theology’s conceit of purposive design, that the thorny problem of explaining the contingent emergence of intricate natural systems can emerge in its full complexity. Works like Darwin’s *On the Various Contrivances by which British and Foreign Orchids are Fertilised by Insects* (1862) must be recognized as crucial developments in the study of how ecological interactions evolve. On the other hand, it is striking that most histories of ecology give scarce attention to Darwin’s contributions. One reason, perhaps, is that later ecological thought, in the hands of theorists like John Phillips, was deeply inflected by organismism. As Arthur Tansley (an advocate of the contrasting “ecosystems” approach) put it, witheringly: the “enthusiastic advocacy of holism is not wholly derived from an objective contemplation of the facts of nature, but is at least partly motivated by an imagined future ‘whole’ to be realised in an ideal human society whose reflected glamour falls on less exalted wholes, illuminating with false light the image of the ‘complex organism’” (“The Use and Abuse of Vegetational Concepts and Terms” 299). To truly appreciate Darwin’s ecological vision, it would be necessary to come to terms with the continued “glamour” of the organism as a governing model for our conception of the earth and its systems.

**IV. Conclusion**

40. In *The Romantic Conception of Life*, Robert Richards has emphasized the important connection between the Darwins by means of their mutual investment in Romantic Naturphilosophie and the organic interconnection of ontogenetic development and phylogeny. The present essay, in line with Goldstein, places the Darwinian imagination in relation to an alternative line of anti-organic thought that was equally Romantic but emerged at the nexus of thinking about the tension between material systems and social organization. As explored by Daniel Stout, this anti-corporate Romanticism scrambled the longstanding notion of the state as a social body, and drew
substantial support both from the complications of corporate personhood and the confused account of causality disclosed by empirical accounts. Here I wish to draw a contrast, emphasized by a range of writers including Gavin Budge, Denise Gigante, and Catherine Packham, between the materialist investments of English Romanticism and German Naturphilosophie. In essence, Charles’s discussion of pangenesis can help us to see what distinguishes Erasmus Darwin’s vital materialism from the organicism envisioned by Kant and others (and laid out, e.g., in recent works by Theresa Kelley and Robert Mitchell). It is a deeply ecological vision, one that emphasizes the interplay between the elements of the organism and its wider world, and it marks a radical departure from green Romanticism and the aesthetics of natural unity.

41. Charles Darwin, by assuming a radically anti-holist, anti-organic ontology, consistently cleared space for more open, more contingent, and ultimately more ecological theories of nature. Some, like the theory of natural selection itself, proved enormously powerful; others, like pangenesis, have not yet found much influence. Though natural selection has been essentially verified by later generations of researchers, pangenesis was quickly discredited, first by his nephew, Francis Galton, and later by both the rediscovery of Mendel’s genetic experiments and the discovery and decoding of DNA. Even so, if the value of a theory is established by its later uses, pangenesis may deserve another look. Pangenesis proved influential in the development of modern gene theory through the work of Hugo de Vries and August Weismann (Holterhoff, “The History and Reception of Charles Darwin’s Hypothesis of Pangenesis”). And in recent years geneticists have turned with excitement to modes of inheritance outside the genetic material of the germ line. In particular, recent research has been focused on two distinct mechanisms of inheritance: environmentally-induced changes to molecules of the “epigenome” that impact gene expression and development; and the inherited “microbiome” – the collection of bacteria, fungi and viruses (with their own genomes) that supports organismic life.36 Both, it turns out, are transmitted to complex organisms by their parents and environment alongside the traditional mechanisms of DNA replication through the germ line. Darwin’s pangenesis imagined the mechanism of inheritance as a kind of swarm of material inherited from distinct cell lines and over distinct time scales, and recent research paints a similar view, locating the traditional mechanism of parental DNA transmission within a larger constellation of molecular and genomic systems of inheritance.

42. For the purposes of this paper, however, I am more interested in what pangenesis can tell us about Charles Darwin’s engagement with his grandfather’s work, and in particular, his grandfather’s contributions to the theory of biological inheritance and development. This essay argues that
Charles’s theory of pangenesis develops a line of thought that posited the autonomy of organismic components. Many thinkers explored the autonomy of living matter and the structures of the organic body, including Bernard, Owen, and especially Erasmus Darwin. Both of the Darwins were fascinated by the problem of inheritance and the question of what the mechanisms of inheritance might tell us about the shared biological basis of all life. If their evolutionary theories posited a common origin to life – from single celled organisms, to plants, to animals – both felt that close study of the mechanisms of reproduction provided evidence for that common origin and the factors that determined differentiation and evolution. Pangeneses demonstrates the longer influence of Erasmus’s epigenetic thought, and especially his effort to describe the basic nature of the organic world.

Pangenesis offers a distinct way of understanding the problem of influence that has long bedeviled studies of the relation between science and literature, and especially, the relation between the Darwins. From the first reviews of On the Origin of Species to recent studies by Desmond King-Hele, studies of the relation between Erasmus and Charles Darwin inevitably turn on the problem of inheritance: biological, scientific, and literary (Wilberforce, “Darwin’s ‘On the Origin of Species’”; King-Hele, Doctor of Revolution; King-Hele, Erasmus Darwin). Ernst Krause, in his brief study of Erasmus, accurately summarized this tendency: “We find the same indefatigable spirit of research, and almost the same biological tendency, as in his grandson; and we might, not without justice, assert that the latter has succeeded to an intellectual inheritance, and carried out a programme sketched forth and left behind by his grandfather” (Krause, Erasmus Darwin 132, emph. added). Such accounts, as Alexis Harley has recently observed, powerfully confuse notions of biological and intellectual relation. While inheritance is a particular problem for studying the Darwins, it has long been a central concern of the study of science and literature, particularly as that field developed from the older history of ideas in the tradition of A. O. Lovejoy and Marjorie Hope Nicolson (Rousseau, “Literature and Science,” 585-6). Gillian Beer effectively reversed the problem of transmission with her influential call to examine the “two-way” traffic by which scientific theories and imaginative models are exchanged between both writers and scientists (Darwin’s Plots 5). More recently, and with the advent of historicist and contextualizing approaches to the problem of cultural history, the “one culture” theorists have sought to locate both scientists and writers within larger determinative contexts (Levine, One Culture “Introduction”). Instead of the integrity of the unit idea or specific strategies of literary representation, such thinking locates the integrity of influence at the level of the culture.
both formulations marked a substantial advance over exclusive study of the influence of new scientific theories upon the literary imagination (as is still common), the Darwins make it hard to explore either two-way exchange or cultural integrity insofar as the first writer died before the second was born.

44. In positing an alternative to the notion of the integrated body (whether polyp or person), Charles Darwin’s theory of pangenesis furnishes a different way of thinking about the problem of inheritance. If we read figures like Erasmus and Charles Darwin less as singular beings, related in their birth and beliefs, than as two nexuses of scientific and literary influences, then the problem of relation becomes far less determinative. As I have tried to show, both writers engaged a wide array of other sources for thinking about the problem of inheritance and generation. On this view, the familial relation between the Darwins might be examined less as a question of descent than as one particularly active conduit among the many that connected the two writers and their works. Works like Zoonomia or The Variation of Animals and Plants under Domestication are strongly linked nodes within a wider network of influences, beliefs, and theses regarding the natural world. Such a vision underlines the extraordinarily accidental nature of such configurations and their relationships. If both of the Darwins might be viewed, in their own right, as “bed[s] of mould full of seeds,” the many intellectual seeds they helped germinate (only some of which they shared) were outnumbered by the many they did not: the seeds that remained dormant, the many more that never found their way into their respective plots of the intellectual landscape. Moreover, to truly see this vision through, we would have to recognize that these fertile constellations of thought are far less stable than the “unit ideas” envisioned by Lovejoy or even the “units of cultural transmission” envisioned by Richard Dawkins (Lovejoy, The Great Chain of Being 3; Dawkins, The Selfish Gene 249). We’d have to recognize each intellectual seed as a little ecology in itself, built up out of smaller elements that are relatively autonomous, and have relatively arbitrary interactions – as either Darwin might put it, as “a little universe … inconceivably minute and as numerous as the stars in heaven” (Variation 2:204). Such imaginative visions prove the fertility of thinking with the Darwins.
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1 Though it seems like an echt modern locution, “Darwinian imagination” was coined derisively in a 1904 translation of a book by Eberhardt Dennert, *At the Deathbed of Darwinism*, 17.

2 Ernst Krause’s brief study of Erasmus Darwin, which Charles Darwin had translated and published, considers their wider thinking about nature as well as the relation between their evolutionary theories, while Samuel Butler’s *Evolution, Old and New*, focused on the latter. (*The Life of Erasmus Darwin; Evolution, Old and New*). For more recent discussions see Desmond King-Hele’s biographies: *Doctor of Revolution; Erasmus Darwin*.

3 Darwin, *The Autobiography of Charles Darwin*, 49.

4 Griffiths, *The Age of Analogy*.

5 Darwin, “Notebook M: [Metaphysics on Morals and Speculations on Expression (1838)].”

6 Even after nearly twenty years of fitful experiments and the collation of supporting facts, Darwin admitted in 1859 that “many and grave objections may be advanced against [his] theory.” Darwin, *On
The case for considering the conceptual grounds of scientific theories and controversies without “picking the winner” has been made in a series of influential works. For examples, see Kuhn, *The Structure of Scientific Revolutions*; Bloor, *Knowledge and Social Imagery*; Shapin and Schaffer, *Leviathan and the Air-Pump*; Daston, “Historical Epistemology.”

In Althusser’s account (now generally accepted), scientific practice is underwritten by basic theoretical and ideological presuppositions, a background understanding or “spontaneous philosophy” that conditions how they think about the world and which questions they ask. Althusser, *Philosophy and the Spontaneous Philosophy of the Scientists*, 116.

Usually realist fiction treats the basic nature and behavior of matter and of living things as a given, rather than a problem. That said, most fiction is definitively concerned with a social ontology. We might take this as its primary subject – even fictions, like Edwin Abbott’s *Flatland*, that do not concern people at all.

Edward Olby’s judgment of Charles’s approach applies equally well to Erasmus’s: both are defined by “the assumption of identity of all forms of reproduction.” Olby, *The Origins of Mendelism*.

Amanda Jo Goldstein has given extensive attention to this debate and its influence on Romantic materialism, including Erasmus Darwin’s. *Sweet Science*, 40-64.

For accounts of the inheritance model, see Charles Darwin and King-Hele, *The Life of Erasmus Darwin*; Butler, *Evolution, Old and New*; King-Hele, *Erasmus Darwin*. For an argument that posits their shared participation in a larger “Romantic conception” of living systems, see Richards, *The Romantic Conception of Life*.

In a separate article, I have detailed how Erasmus Darwin’s later works, especially *Phytologia* (1800) and *The Temple of Nature* (1804), exchange the epigenetic paradigm for a new model of sympoietic development drawn from Claude Berthollet’s theory of double elective affinity. Griffiths, “The Distribution of Romantic Life in Erasmus Darwin’s Later Works.” See also Adler, “Goethe’s Use of Chemical Theory in His Elective Affinities.”

Needham remains the foundational treatment of the longer history of embryology from the classical period on. *A History of Embryology*.

As Martin Priestman has shown, this kind of intervention in classical discussions is a hallmark of Erasmus Darwin’s writing. See *Romantic Atheism*, 67–74.
While Erasmus explicitly cites Aristotle’s *History of Animals*, his reference to Aristotle’s discussion of mules is drawn from *On the Generation of Animals*.

See Sandler and Sandler, “A Critical Ambiguity That Contributed to the Neglect of Mendel’s Paper.”

For accounts of the relation between microscopic observation, preformation and *emboîtement*, see Ruestow, “Leeuwenhoek and the Campaign against Spontaneous Generation”; Bowler, “Preformation and Pre-Existence in the Seventeenth Century”; Pyle, “Animal Generation and the Mechanical Philosophy”; Cheung, “The Hidden Order of Preformation”; Rieppel, “The Reception of Leibniz’s Philosophy in the Writings of Charles Bonnet (1720-1793).” See also Denise Gigante’s discussion in *Life*, 9–13.

As I have argued elsewhere, Erasmus Darwin’s *The Botanic Garden* insists on a coherent and interwoven model of evolutionary development that operates at all natural scales and across seeming distinct natural divides, a common vision in which the development of seeds, eggs, planets and nebulae is driven by the same basic pattern of development and transformation. Griffiths, *The Age of Analogy*, chap. 1.

Griffiths, “The Distribution of Romantic Life in Erasmus Darwin’s Later Works.”

See discussions in Vorzimmer, “Charles Darwin and Blending Inheritance”; Geison, “Darwin and Heredity”; Hodge, “The Darwin of Pangenesis.”

“Referring to the doctrine of physiological units which the preceding chapters work out, [Darwin] at first expressed a doubt whether his own was or was not the same, but finally concluded that it was different.” Spencer, *Principles of Biology*, 1:356.

Darwin, *The Variation of Animals and Plants under Domestication.*, 2:375. All further references given parenthetically by volume and page number.

Spencer’s *Principles of Biology* begins with the claim that life is defined by the movement toward an equilibrium that responds to external forces and actions. The first volume of Darwin’s *Variation*, by contrast, is filled with the various and bizarre breeds of pigeons, pigs, and other animals that depart wildly from original stock.

One reason – which I will elaborate later in this essay – seems to be that Erasmus, like his contemporaries was committed to the notion of the organism as an aesthetic unity. At the same time, we might view this as an implication furnished by his poetry, insofar as it explores floral life as a system of interacting and relatively autonomous sexual parts, the sex organs of the plants, figured as nymphs and swains, become little microcosms of larger social formations.
Hence his insistence on the organ’s “vie propre” or “autonomie” in the passage Darwin cites. (Bernard, *Tissus vivants*, 22. Further references given parenthetically by page number.) Bernard was the major source, for instance, of the tissue theory that George Eliot attributes to Tertius Lydgate in *Middlemarch*. Bernard also believed that the proper study of tissues required two perspectives: on the one hand, it was crucial to study the place of the organ or tissue within the larger living body, (that is, its *organic* relations); but he felt it was equally important to study the conditions or *milieu* in that produce specific activities by the tissue or organism, (its *environmental* relations). His perspective, if not strictly ecological, yet emphasized the dependence of organic organization on environment.

Erasmus Darwin notably moves toward a more distributed model of organic life in *Phytologia*, which elaborates a more ecological notion of living bodies, based on the notion of double elective affinity, the subject of Goethe’s 1809 novel, *Die Verwandtschaften*. Griffiths, “The Distribution of Romantic Life in Erasmus Darwin’s Later Works.”

Darwin and King-Hele, *The Life of Erasmus Darwin*, 40. As this was written a decade after *Variation*, and after an extensive review of Erasmus’s writing, it is unclear whether Charles had read *Phytologia* before theorizing pangenesis.

Lyell, “15 Mar. 1863 Letter to Charles Darwin.”

Lyell, “9 Mar. 1863 Letter to Joseph Hooker.”

Latour, *Science in Action*; Latour, *We Have Never Been Modern*; Latour, *Pandora’s Hope*.

Beer, *Darwin’s Plots*; Levine, *Darwin and the Novelists*.

On the one hand, Kant noted that the tree “generates itself as an individual” but in a manner “entirely distinct from any other increase in magnitude in accordance with mechanical laws.” On the other hand, you may graft different portions of a tree onto different parts, so that “one can regard every twig or leaf of one tree as merely grafted or inoculated into it, hence as a tree existing in itself” so that “the preservation of the one is reciprocally dependent on the preservation of the other.” Kant, *Critique of the Power of Judgment*, 242–43.

Ian Duncan, “Aesthetics and Form in Charles Darwin’s Writings” *Oxford Research Encyclopedia, Literature* (Feb, 2017): 3.

Yuan and Zhu, “Histone Variants and Epigenetic Inheritance”; Huang, Xu, and Zhu, “Epigenetic Inheritance Mediated by Histone Lysine Methylation”; Campos, Stafford, and Reinberg, “Epigenetic Inheritance”; Sen et al., “Multigenerational Epigenetic Inheritance in Humans”; Human Microbiome
Project Consortium, “Structure, Function and Diversity of the Healthy Human Microbiome”; Human Microbiome Project Consortium, “A Framework for Human Microbiome Research.”