Review of: "Femmes finales: natural selection, physiology, and the return of the repressed"

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Potential competing interests: No potential competing interests to declare.

I admire how the geneticist David Haig has taken up the historian's charge in interpreting the mindsets of key figures in 19th century British biology as they confronted causation and the appearance of purpose in living systems. He has shown convincingly how their various scientific perspectives intersected with their received belief systems in producing a body of often conflicting assertions (including appeals to a culturally laden virgin/mistress dichotomy) some of which proved surprisingly influential beyond their times.

My own aim in providing these comments is somewhat orthogonal to David Haig's. As a non-historian, I will take the liberty of assuming the past figures had similar motives to present-day biologists: explaining form and function with recourse to as few unjustified assumptions, and with as close adherence to first principles, as possible. I therefore permit myself to make use of newer science to dispel what I take to be errors of past thinkers. This is not too different from Haig's observation that most biologists who followed Darwin (and evidently, he himself) accept that "natural selection provided an alternative to design."

As I try to discern the consequences to their intellectual frameworks of what the 19th century figures didn't understand, this comes with the recognition that there are still major lacunae in knowledge that make our own picture also profoundly incomplete. Like our predecessors, we tend to fill these in with (nowadays mostly secular) tenets of faith (e.g., adaptationism, gene-centrism) but these are increasingly controversial. Thankfully, sexualized metaphors are no longer in fashion.

Some points to consider:

1. Haig describes the 19th century turn by physiologists toward "explanations in terms of physics and chemistry," leaving morphology (at least until Darwin) in the province of final cause and purpose. But physics is not just the science of small-effect processes like Aristotelian impetus or Newtonian inertia. It also pertains to properties of qualitatively different forms of matter, many of which, on the biology-relevant mesoscale, exhibit large-effect transformations. Indeed, chemistry itself is a branch of physics, one whose reactions (as Haig quotes T.H. Huxley as noting) provide an analogy for saltational transitions between disparate organismal types. With the rise of thermodynamics and the theoretical analysis of transport processes, the characterization of irreversible phenomena such as diffusion, viscous flow and phase transitions made the idea that developmental morphogenesis was an unsuitable subject for physical explanation only tenable for those unfamiliar with the new physics of their time.
2. Similarly with design. Haig justifiably expresses dissatisfaction with William Whewell's unwillingness to attribute design

to the outcome of physical processes such as mineral crystallization or the law of gravity. But even objects subject to the then familiar Newtonian laws of motion and gravitation can transition between parabolic, elliptical, and hyperbolic motion, representing distinct morphological motifs, dependent on initial conditions. The periodic table of the elements (ca. 1863, with partial versions advanced earlier) demonstrated that a finite set of atoms of discrete qualities, a chemical "pattern language" in the term of the architectural theorist Christopher Alexander – could arise in the nonliving world by purely physical effects. The physically ordained endpoints (the distinct atoms) represent the manifestation of a kind of final cause, but one based on the latent inherent properties of certain material systems. Could not biological types (plants, animals, phyla within the animals) arise by similar means, albeit in systems of much greater complexity? Earlier "rational morphologists" like Goethe and Geoffroy Saint-Hilaire thought so, as did later, more physically sophisticated scientists like William Bateson and D'Arcy W. Thompson. Haig notes that "Whewell conceded that Owen's homologies and archetypes (particularly regarding the vertebrate limb skeleton) "necessarily displace some of the old views regarding Final Causes." The recognition that the limb archetype and its homological variants were effects of a self-organizing physical process (the pattern-forming reaction-diffusion mechanism described by the mathematician Alan Turing) involving the secreted products and cells of embryonic limb tissue, was more than a century and a half in the future. But the resulting reconciliation of unity of type and conditions of existence owed nothing to the theory of natural selection.

3. Haig states "The elimination of final causes from physics and chemistry was largely completed by the beginning of the nineteenth century but final causes were still regularly invoked in biology and medicine." I question this assertion regarding physics and chemistry based on the atomic structures of the chemical elements, which did not appear simultaneously in the natural world but evolved in a (physically) preordained fashion as the universe cooled. Further, the symmetry-breaking self-organizing physical and chemical systems described and analyzed by Turing, Zhabotinsky, Prigogine and others (generating repetitive stripe- and spot-like arrangements of chemicals), and the multistable dynamical systems studied by other 20th century mathematicians and mathematical physicists, show that nonliving matter can exhibit goal-directed behaviors. The described initiative by 19th century physiologists to assimilate their field to the physical sciences, leaving evolutionary morphology in the realm of purpose, which was affirmed by Huxley, who thought Darwin had the answer to purpose (Haig quotes him, "Physiology and Ontology are two sciences which cannot be too carefully kept apart; there may be such entities as causes, powers, and forces, but they are the subjects of the latter, and not of the former science;" he also cites John Burdon Sanderson's claim that the *Origin of Species* had severed physiology from evolutionary biology) has not held up. Development is now known to occur by processes traditionally thought of as purely physiological: biochemical oscillation (somitogenesis and other forms of segmentation), bioelectricity (stabilization and regeneration of organ morphology) and contractility (gastrulation in some forms), to name a few. The mixing and remixing of these physiological effects in nascent tissues provide morphological variants sufficient to span phyletic boundaries, something difficult to demonstrate for the gradualism favored by the modern synthesis. The question then becomes: can these variants establish themselves in the biosphere?
4. Haig contends that "it was Darwin's *neutralization* of [the argument from design] by exclusion that led to the rapid acceptance of descent with modification. Natural selection provided an alternative to design." But Darwin's complete dependence on "contrivances and beautiful adaptations [being] slowly acquired through each part occasionally varying

in a slight degree in many ways" (quoted from his 1862 book on the fertilization of orchids) put him in the position of his grandfather: not the evolutionist poet Erasmus Darwin, but the pottery manufacturer Josiah Wedgewood. The latter, being ignorant about the physics of ceramics and the chemistry of colorants needed thousands of attempts to arrive at his famous Jasperware of Wedgewood blue. Darwin's theory explains the design of organisms as products of trial and error like his grandfather's pots. The organismal types within which variation occurs have no rhyme or reason beyond the fact that they have survived. Darwin's answer to how the (marginally different) variants of his hypothesis established themselves in the biosphere was that some performed slightly better at the tasks that all their populational cohorts were engaged in, and thus left more offspring. But, as Haig says, "[t]here might be other alternatives."

5. One such alternative, a challenge to the relative fitness-based engine of Darwinian natural selection, is that organisms have agency, that is (in the formulation of Richard Lewontin) they are subjects, not only objects, of evolution. This would mean that even if the "contrivances" of a class of organisms arose abruptly, due to genes of large effect or the retuning of developmental physiology by environment change, the remarkable correspondence between these features and the resources the organisms use and the external challenges they face were not necessarily built up gradually over vast amounts of time. The organisms, potentially finding themselves with a new structural or functional trait, being agents, would actively seek out previously unexploited niches containing corresponding affordances. While natural selection might be the way microevolution occurs (e.g., the reshaping of finches beaks), the saltational effects of developmental reorganization, in conjunction with organismal agency and invention of new niches, could explain macroevolutionary events of the past, e.g., the origination of new phyla.
6. Where did organismal agency come from (assuming it is a thing)? Can it be explained by successive cycles of microevolution acting on non-agential prebiotic chemical systems? This is an entrenched supposition of most present-day biologists – if not natural selection what else is there? There are other possibilities, though. Perhaps it is an exotic emergent property of a novel form of matter (derived from other forms of matter). Unprecedented material properties first appeared in nature with the advent of atoms, black holes, superconducting fluids, biomolecular condensates… Anyone who entertains alternatives to selectionism should take care, though. Unconventional views in biology are no longer likened to secret mistresses, but when it comes to evolution some notions are still treated as shameful.