Monism and Morphology at the Turn of the Twentieth Century*

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Sander Gliboff, Indiana University

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Introduction

Early in 1893, not long after giving the public lecture that would become a small book on monism as the link between science and religion,[1] Ernst Haeckel (1834–1919) began to think about scaling back his research efforts in morphology and systematics. He wrote to his friend Thomas H. Huxley in England that he would prefer to:

> Fill up the rest of my days with general studies, particularly of monistic philosophy. The fight against clericalism and the Medieval stupefaction of our so-called "educated" elite [*Gebildeten*]

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1. Ernst Haeckel, *Der Monismus als Band zwischen Religion und Wissenschaft: Glaubensbekenntnis eines Naturforschers*, vorgetragen am 9. Oktober 1892 in Altenburg beim 75-jährigen Jubiläum der Naturforschenden Gesellschaft des Osterlandes, 15th ed. (Leipzig: Alfred Kröner, 1911).

> (—theologians, jurists, philologists, etc.—) is becoming ever more important.[2]

After one more book on phylogeny (his *Systematische Phylogenie* of 1894), he carried out his intentions and produced his well-known, popularizing monistic works, such as *Die Welträtsel* (1899) and *Die Lebenswunder* (1904).

These works were so well known and influential that it is easy to forget that monism was not a late interest of Haeckel's that he took up only in semi-retirement. From his *Generelle Morphologie* of 1866 on, monism had been an integral part of his morphological work and his interpretations of evolutionary theory. Specifically, as I shall emphasize in this essay, it entered into his conception and formulation of the causes of variation. Under monism, the admissible causes of variation could not include either divine providence or any influences of the organism's own purposes, mind, spirit, or just about any internal initiative. The causes of variation were external, and evolution was just another natural process, driven by changes in the environment, with no more plan or purpose than the weather. For years, Haeckel expended a great deal of energy combatting excessively internalistic causes, which he always treated as threats to monism.

From the 1890s on, however, Haeckel's interest in these issues flagged, and it was left to younger monistically oriented morphologists and evolutionists to

2. Letter of 22 January 1893 to Thomas H. Huxley, in Georg Uschmann and Ilse Jahn, "Der Briefwechsel zwischen Thomas Henry Huxley und Ernst Haeckel: Ein Beitrag zum Darwin-Jahr," *Wissenschaftliche Zeitschrift der Friedrich-Schiller-Universität Jena, mathematisch-naturwissenschaftliche Reihe* 9, no. 1/2 (1959/60): 27.

defend the primacy of external causes and to respond to new challenges in the early twentieth century. Haeckel's student Richard Semon (1859-1918), for example, broke his lance against Mendelian genetics and developed his *Mneme* theory of organic memory as an alternative that would allow the environment to induce new variation. The theory then explored ways in which protoplasm might store the response for later recollection and repetition in development. Ludwig Plate (1862-1937), who took over Haeckel's chair at the University of Jena and became an influential commentator on new research on heredity and evolution, used his influence to fend off a variety of threats to the role of external causes, coming from theistic evolution, orthogenesis, and psycho-Lamarckism. Paul Kammerer (1880-1926) took a third tack and appropriated the new methods of experimental morphology and genetics in order to defend the conception of Darwinism he had learned from his friend Semon and his reading of Haeckel. He wanted to demonstrate experimentally that the environment could indeed induce adaptive changes, and that the changes gradually would become fixed in heredity in the form of Mendelian genes on chromosomes. Later still, I suggest, traces of their reasoning and Haeckel's can be found in the evolutionary synthesis as well as in later evolutionary thought, and that an argument could be made for some strong continuities from Haeckel to the present in this question of the causes of variation and the limits to the changes the organism can initiate on its own.

Monism and Mechanism in Haeckel's Evolutionary Morphology

From the very first page, in the dedication to his Jena colleague Carl Gegenbaur, Haeckel made it clear that *Generelle Morphologie* was intended above all to be a "mechanical morphology" and a monistic one. In the foreword, he went on to explain that, as he saw it, there were two completely separate categories of natural science: the sciences of the inorganic, plus physiology, which were monistic and mechanistic, and aimed to discover causes; and morphology, development and evolution [*Entwicklungsgeschichte*], and anatomy, which were dualistic, vitatlistic and searched for teleological pseudo-explanations [*zwecktätige Scheingründe*]. The purpose of his book was:

> To force all this disastrous and fundamentally backward dualism wholely out of every field and subfield of anatomy and development, and, through mechanical-causal grounding, to raise the entire science of the developed and the developing forms of organisms to the same solid height of monism, in which all the other sciences, long or not so long ago, found their unshakeable foundation.[3]

3. Ernst Haeckel, *Generelle Morphologie der Organismen: Allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanisch begründet durch die von Charles Darwin reformierte Descendenz-Theorie*, 2 vols. (Berlin: Georg Reimer, 1866), xi–xv, quote on xiv-xv.

Haeckel proposed to follow Darwin's lead and use his theory to rid biology of everything that he thought smacked of the mystical or miraculous, from overt Creation myths and fixity of species to pseudo-scientific forms of vitalism, teleology, organizing principles, or creative forces:

> We see in Darwin's discovery of natural selection in the struggle for existence the most striking evidence for the exclusive validity of mechanically operating causes in the entire field of biology. We see in it the definitive death of all teleological and vitalistic interpretations of organisms.[4]

Still, Haeckel was not satisfied with the way Darwin's principles had been applied so far. There were some soft spots that needed to be hardened in order to keep teleology and divine providence at bay, and some of them had to do with the nature and causes of variation.

The Nature of Variation

In *The Origin of Species*, Darwin gave at least three different explanations of variation. Two were the ones that are now more often associated with Lamarck, namely that variation arose from the direct effects of the environment on the organism, and from the habitual use or disuse of organs. The third was that it resulted from the general instability of the reproductive system of the parent, which failed, for reasons that were seldom apparent, always to make perfectly

4. Ibid., 1: 100.

similar offspring.[5] Haeckel had no objections to any of these, but added some restrictions on how much the organism itself—not just its mind or purposes, but also its internal mechanisms of heredity, growth, and development—could contribute to the process of variation, and how much depended upon external stimuli coming from the environment. These restrictions derived from monistic principles in addition to the practical demands of morphology.

Consider this description of the interplay between the internal, biological continuity that was provided by heredity and the environmental stimuli that caused variation and adaptation:

> Of these extremely important phenomena. . . heredity rests upon the immediate material connection between the parental and the newly arising organism. Inasmuch as the latter always retains a part of the former, the same functions must necessarily manifest themselves through that same material. This is the basis for heredity, because of which every organism is similar to its parental organism.[6]

Note that heredity was a conservative processes. It accounted for material continuity and similarity in form within a lineage, but did not introduce anything new.

A distinct, external process introduced novel variation:

5. Charles Darwin, *On the Origin of Species by Means of Natural Selection: Or the Preservation of Favored Races in the Struggle for Life* (London: John Murray, 1859), URL: `http://darwin-online.org.uk` (accessed 07/22/2008), from The Complete Works of Charles Darwin Online, 7-13.

6. Haeckel, *Generelle Morphologie*, see n. **??**, 1:151-2.

> Another circumstance works against the absolute identity between both [i.e., offspring and parental individuals], namely that the youthful organism that comprises only a portion of the parental is forced to complete itself on its own, through growth, up to a certain point. Now inasmuch as this independent nutrition of the organic individual, which is based on the simplest mass attraction of the surrounding nutritive substance, is influenced by the surrounding conditions of existence (temperature, extension and surface area of solid bodies in the environment, etc.),... there arises a certain degree of variability, of changeability in the quantity of assimilable material that enters into the absorptive [*imbibitionsfähig*] organism and completes the growth of the individual.[7]

It is quite significant here, from the monistic point of view, that environmental influences triggered variability, not the organism or anything in it. Coming from outside the organism, the causes of variation were independent of any sort of mind, spirit, vital force, purposes or anything else that might reside within. This provided an additional bulwark against certain forms of teleology: not only do those dualistic entities not exist, but even if someone were to think they did, they still would have no agency in generating variation. This solution also made good biological sense, because it helped account for the obvious messiness of ontogeny and phylogeny—and especially because it provided mechanisms of

7. Ibid., 1:152.

producing individual variation and brought Haeckel's system into line with Darwinian theory.

According to Haeckel, environmental conditions were so many and varied that no two individuals would ever experience them and react to them in precisely the same way: "*No organic individual remains absolutely the same as the others* [Emphasis original]"[8] he wrote. Thus, Haeckel's system was capable of generating all the variation a selectionist could have wished for.

Finally, Haeckel reinterpreted the Darwinian mechanism of change in terms of a certain antagonism between the conservative internal process of heredity and the potentially progressive and adaptive external influences of the environment:

> Upon this individual variability rests the capacity for adaptation to surrounding conditions of existence, which conditions work against absolute and general heredity, and in their interaction with heredity produce all the diversity [*mannichfaltigkeit*] of the organism-world, according to the laws developed by Darwin.[9]

Again, the key to Darwinian variation and evolution is in the *interplay* between the internal, ancestral heritage and the present-day external environment. Heredity was not "absolute and general," but vulnerable to environmental disruptions.

8. Ibid., 2: 192.

9. Ibid., 1: 152.

The Problem With Internal Causes

Haeckel was always suspicious of systems that gave too much agency to the organism, its constitution, or internal processes of growth and development. For example, he objected strenuously to the theory of botanist Karl Wilhelm von Nägeli, because it had internal, physiological processes driving the plant to ever greater complexity and perfection, with little or no regard to what was going on in the environment. Even though Nägeli couched his description of the hypothetical process in mechanistic terms, the argument still had teleological implications for Haeckel, because the impetus for change was coming from within the organism.

> With Nägeli's assumption "that the organism has a tendency within it to transform itself into a more complexly structured one," we end up on the slippery slope of teleology, upon which we slide helplessly into the abyss of dualistic contradictions and distance ourselves entirely from the single possible mechanistic, natural explanation.[10]

Haeckel thought that Nägeli overestimated the perfecting tendencies of nature and made progress seem pre-ordained and inevitable, when it clearly was not:

> We can be even less inclined to decide in favor of accepting such a special, as yet entirely inexplicable perfecting principle, because the selection theory explains the mainly progressive direction of differ-

10. Ibid., 2: 264.

> entiation... very well, and because, in addition, the retrogressions that occur everywhere show that progress is in no way exclusive or unconditional.[11]

A different anti-monistic ramification of internal causes was at issue in the dispute between Haeckel and embryologist Wilhelm His in the 1870s. His' approach was to describe embryonic development in terms of internal mechanical operations such as pushing and pulling and folding of tissue, each operation physically causing the next in an unbroken chain of causes and effects, from the egg to the adult. In a provocative thought experiment, he guided the reader through the mechanical steps in the development of a chick *in reverse*, describing how one might take a four-day old chick embryo, and by cutting and unfolding and shrinking, transform it step by step back into the shapes of earlier stages.[12]

What I think most irked Haeckel was the claim that one could, in principle, transform any adult animal mechanically all the way back to the fertilized egg and even trace specific adult body parts to specific regions of the egg. Then, since the egg resulted from mechanical operations too, its origin could be traced back through the previous adult to the previous embryo to the previous egg, and so on. Hence, the history of life was nothing but a chain of such mechanical operations, stretching all the way back to the origin of life. Working forwards,

11. Ibid., 2: 264.

12. Wilhelm His, *Unsere Körperform und das physiologische Problem ihrer Entstehung* (Leipzig: F. C. W. Vogel, 1874), 1-19; see also Wilhelm His, "Die Häute und Höhlen des Körpers," *Archiv für Anatomie und Physiologie, anatomische Abteilung* (1903): 368–404, reprint of an 1865 article.

if you knew the structure of the first organisms and the laws of embryological mechanics, you could predict evolutionary history. You did not need to know anything about the environment.

Haeckel did not take this sitting down. He wrote that there was an "unbridgeable chasm" between himself and His and that His approached embryology like a tailor, who only understood how to fold and cut and reattach material. Haeckel thundered that:

> Either a direct, causal connection between ontogeny and phylogeny exists or it does not exist. Either Ontogeny is a condensed excerpt of phylogeny or it is not. Between these two assumptions there is no third one! Either epigenesis and descent or preformation and Creation! [Emphasis original][13]

In Haeckel's dichotomy, His had to be on the side of preformation and Creation, because he traced the causes of ontogeny and phylogeny back to initial conditions, and restricted Nature's creativity to the mere working out of preexisting potential. Haeckel demanded a process that would continually intervene in the history of life to break up the chain of deterministic causes. Unpredictable physical forces in the environment were what introduced novel variations and adaptations and saw to it that nature not be restricted to a single creative moment long ago.

13. Ernst Haeckel, "Die Gastraea-Theorie, die phylogenetische Classification des Thierreichs und die Homologie der Keimblätter," *Jenaische Zeitschrift für Naturwissenschaft* 8 [= NF 1] (1874): 1–55, 6-9.

It should be noted, however, that there were limits to the transforming power of the environment. It produced variations on an ancestral theme, not a wholesale reinvention of the organism—otherwise Haeckel's practical program of reconstructing ancestry and phylogenetic relationships could not be justified. Heredity had to preserve something of the sequence of past adaptations and make the embryo run through it, more or less reliably, in development. So, I wish to emphasize that Haeckel did not reject internal causes altogether, but struck a certain balance and allowed for a great deal of interplay between the internal and the external.

New Challenges and Champions of Monism in the Twentieth Century

Haeckel's monistic system of morphology was not without its weaknesses. One was Haeckel's optimism about progress. He did not make variation "random" in the modern sense, even though it was unpredictable. He wrote as if the deck were stacked toward adaptive changes. In fact, Haeckel used the terms "adaptation," "progressive heredity" and "variation" interchangeably, at least in his early works. Perhaps all this meant was that the unfavorable variations were of no practical importance in morphology. One did not see them recorded in heredity and being recapitulated in the embryo, because natural selection eliminated them promptly. But if Haeckel is taken literally on the general favorability of variation, his argument could be turned on its head and used as evidence that the

organism responded purposefully to the environment. That was, in fact, one of the counter-arguments used by the theistic evolutionist Erich Wasmann in 1907.

Further challenges came from within mainstream biology. August Weismann's neo-Darwinism and germplasm theory sought to isolate the hereditary material from the kinds of environmental influences that Haeckel relied upon for generating variation, and called attention to the lack of specifics in Haeckel's system about the internal mechanisms of heredity. The experimental turn in biology, especially in the study of development (*Entwicklungsmechanik* or developmental mechanics), shifted attention away from historically contingent environmental effects back to the internal workings of the embryo. The rediscovery of Mendel and the rise of classical genetics also focused on the internal, leaving considerable uncertainty about the role of the environment in producing mutation. Increasingly, however, it was not only—or mainly—Haeckel himself who responded, but rather a younger generation of monistic evolutionists.

Ludwig Plate

Wasmann in Berlin, 1907

In his high-profile books and public lectures on evolution and religion, Erich Wasmann stood out among all the critics of monism for his impressive credentials as both a naturalist and a theologian.[14] He did pathbreaking work on

14. E.g., Robert J. Richards, "Ernst Haeckel and the Struggles over Evolution and Religion," *Annals of the History and Philosophy of Biology* 10 (2005):

the morphology, behavior, and even evolution and of ants and their commensals, and he was also a Jesuit priest, who was at least perceived to speak for the Catholic church.[15] He went a long way with the evolutionists, giving evolutionary interpretations of life in ant- and termite colonies, and allowing that natural selection played at least some role in the evolutionary process. In his rebuttals to Haeckel and the monists, he did not have to resort only to arguments about general principles—the nature of matter and eternity, and the like—but also discussed the mechanisms of evolution.

In a 1907 series of public lectures in Berlin,[16] which, he insisted repeatedly, was not intended as a counterattack in kind against Haeckel's lectures at the same venue two years previously,[17] Wasmann homed in on the issue of internal and external causes of variation, and its ideological ramifications. He realized

100-102; Heike Barantzke, "Erich Wasmann (29.5.1859–27.2.1931): Jesuit und Zoologe in Personalunion," *Jahrbuch für Geschichte und Theorie der Biologie* 6 (1999): 77–140.

15. His accommodation of evolution actually got him into trouble with his superiors, but that was not generally known at the time: Barantzke, see n. **??**.

16. For the time being, I rely on the account compiled and edited by Ludwig Plate Ludwig Plate, ed., *Ultramontane Weltanschauung und moderne Lebenskunde, Orthodoxie und Monismus: Die Anschauungen des Jesuitenpaters Erich Wasmann und die gegen ihn in Berlin gehaltenen Reden* (Jena: Gustav Fischer, 1907); on Wasmann as an opponent of Haeckel's see also Abigail Lustig, "Erich Wasmann, Ernst Haeckel and the Limits of Science," 121 (2002): 252–259.

17. Ernst Haeckel, *Der Kampf um den Entwicklungsgedanken: Drei Vorträge, gehalten am 14., 16. und 19. April 1905 im Saale der Sing-Akademie zu Berlin* (Berlin: Georg Reimer, 1905); In English: Ernst Haeckel, *Last Words on Evolution: A Popular Retrospect and Summary*, trans. Joseph McCabe (London: A. Owen, 1906).

that Haeckelian monists had to limit the effects of inner laws and causes, so he tried to show that they could not actually do so. Purposeful responsiveness was implicit in the very notion of environmentally induced variation:

> Let us now go somewhat further into the inner developmental laws of the organic world. On this, we will be answered by the monist side, that we do not need such "inexplicable inner developmental laws!" But if one goes just so far as to assume the responsiveness [*Reaktionsfähigkeit*] of living substance to external stimuli, then one immediately faces a thoroughgoing *purposiveness* [*Zweckmäßigkeit*] that cannot be explained away, simply because the teleology [*Zielstrebigkeit*] is already in there. But I must say, frankly: *The inner developmental laws are in there, too!*[18]

Even under monistic assumptions, Wasmann argued, environmental forces alone could not reshape the organism. Its living substance had to respond in some way, as this response had to be purposeful if it were to produce favorable variations.

On the other hand, Wasmann had to fend off the criticism that he was proposing a deterministic view of evolution, in which everything ran according to those internal developmental laws, which miraculously produced adaptive changes just when they were needed. Here he offered a balance between the internal and the

18. Erich Wasmann, "Theistische und atheistische Entwicklungslehre; Darwinismus und Entwicklungslehre," II. Vortrag des P. Wasmann, am 14. Februar im Oberlichtsaal der Berliner Philharmonie, in Plate, *Ultramontane Weltanschauung*, 31-32, emphasis original.

external to rival Haeckel's:

> By the way, it would be completely backwards to construe the inner developmental laws, which the Christian world view assumes to be the main and fundamental principle of the evolution of the organic word, as an already fully wound-up clockwork that on has to run down. A "pre-stabilized harmony" between organism and environment is also not to be assumed; no, the interaction, the tendency toward interaction, is the thing that allows the inner and the outer developmental factors to work together.[19]

Wasmann then drove home the point that the monist side was already assuming inner, teleological processes in its account of variation:

> That which is called the irritability [*Reizbarkeit*] of protoplasm, the capacity to respond to external stimuli, that is identical to the inner developmental laws. These laws are steered into certain pathways by external influences and fixed through heredity. By this process, there originate ever more specialized developmental directions that rest, most fundamentally, on the same *internal* basis from which they started out.[20]

He gave them no credit for any complex interplay between the internal and the external, but portrayed the Darwinian theory as purely and unjustifiably exter-

19. Ibid., 32.

20. Ibid., 32, emphasis original.

nalisitc: "Therefore, the inner developmental laws are not to be denied, as has often been done by the Darwinian side before and as is still being done."[21] The burden was then on the Darwinian side to show how they could take internal causes into account and have them generate favorable variations, without them being purposeful.

Plate's Monistic Response

In response, Plate refused to let Wasmann pose as a Darwinian (no matter how critical a one) and an anti-Darwinian at the same time. The very idea of an "immanent teleology" that, as Wasmann would have it, made sure that "the changes that occurred under new conditions always turned out to be on the purposive side"[22] was inherently vitalistic. It was not only incompatible with the monistic interpretation of Darwinism, but also, Plate argued, plainly false on empirical grounds.

In contrast to Haeckel's earlier optimistic rhetoric about the progressive and positive nature of most variation—which Wasmann was turning against him and making into an argument for teleology—Plate now made it crystal clear that organisms generally were *not* capable of responding constructively to environmental conditions for which they were not already adapted:

> What if we bring an organism into quite new and unusual conditions,

21. Ibid., 32.

22. Ludwig Plate, "Rede des Herrn Prof. Plate," in Plate, *Ultramontane Weltanschauung*, 64.

> under which neither it nor its ancestors had ever found themselves before? What does it do then, if the conditions are harmful? Does it always act in a way that turns out to be beneficial? Does it always, or at least for quite the most part, react purposively, or does it react extraordinarily often in a purposeless way? Now you all know that the organism, under quite new conditions, reacts almost regularly, alas, alas, in a purposeless way.[23]

In a footnote, Plate had many examples of organisms failing to deal adequately with environmental challenges, dying of exposure to environmental challenges instead of becoming modified by them. Most important, no matter how they dealt or failed to deal with the environment, organisms did as the laws of chemistry and physics dictated. Neither they nor any hypothetical purposive principle in them could possibly have any choice in the matter.

Well, then, how could purposeful adaptations result from such a purposeless, deterministic system? The key is in variation. History has made all individuals different, because they and their ancestors have had unique exposures and responses to their environments. If there is enough variation, some of the variants will just happen to be favorable, and this will not require any special explanation.

> The answer can only be given in the sense of Darwin: in times of need, the individuals of a species never react all in the same way, these so and those so, because they are always somewhat differ-

23. Ibid., 65.

> ent in their inner constitutions; therefore, the ones who chance to change themselves in a purposeful way are preserved and transmit their good characteristics through heredity.[24]

Plate on Orthogenesis and Psycho-lamarckism

The same monistic reservations about internal causes may be found throughout Plate's works. He had made his debut as critical analyst of trends in evolution and heredity with an 1899 lecture on natural selection before the German Zoological Society. The text of the lecture went through several incarnations as an article and grew into an oft-revised book, whose title varied somewhat over the course of several editions.[25] The repeated revisions, along with Plate's editorializing in the *Archiv für Rassen- und Gesellschafts-Biologie*, show how a Haeckelian monist passed judgment on the latest developments in heredity and evolutionary theory. Although he avoided giving credit to Haeckel as much as

24. Ibid., 67n.

25. E. g., Ludwig Plate, *Über die Bedeutung des Darwin'schen Selectionsprinzip und Probleme der Artbildung*, 2nd ed. (Leipzig: Wilhelm Engelmann, 1903); Ludwig Plate, *Selektionsprinzip und Probleme der Artbildung: Ein Handbuch des Darwinismus*, 4th ed. (Leipzig and Berlin: Wilhelm Engelmann, 1913). He later supplemented the book with a shorter, popularizing account and a more specialized treatment of genetics: Ludwig Plate, *Die Abstammungslehre: Tatsachen, Theorien, Einwände und Folgerungen in kurzer Darstellung*, 2nd ed. (Jena: Gustav Fischer, 1925); Ludwig Plate, *Vererbungslehre: Mit besonderer Berücksichtigung des Menschen, für Studierende, Ärzte und Züchter*, 2 vols. (Jena: Gustav Fischer, 1913); Ludwig Plate, *Vererbungslehre: Mit besonderer Berücksichtigung der Abstammungslehre und des Menschen*, 3 vols., 2nd ed. (Jena: Gustav Fischer, 1932–1938).

he could, and he softened the polemics against religion, Plate continued to hold Haeckel's line against inner causes of change.[26] He used the terms "autogenesis" and "ectogenesis" to strengthen the distinction between internally and externally driven variation, and he followed Haeckel in identifying the former with vitalism and mysticism. Accordingly, he attacked most new saltational and orthogenetic theories, as well as the "psycho-Lamarckism" that came into vogue after 1905.

The psycho-Lamarckians, who also called themselves "Eulamarckians" took their cues from August Pauly, a professor of forestry in Munich, who argued that the animal psyche played an active role in recognizing and assessing its needs and initiating the appropriate morphological change and adaptation.[27] Plate answered them in good Haeckelian style, relegating them to the fringes of scientific respectability as long as they gave any hint that the psyche had a non-material existence, independent of, and prior to, the evolution of the brain. The psyche was a product of evolution and could not be its cause.[28]

26. On Plate's career and relationship to Haeckel and to modern Darwinism, see also: Georgy S. Levit and Uwe Hoßfeld, "The forgotten 'old-Darwinian' synthesis: The evolutionary theory of Ludwig H. Plate (1862–1937)," *NTM—Internationale Zeitschrift für Geschichte und Ethik der Naturwissenschaften, Technik und Medizin* 14 (2006): 9–25; Gloria Robinson, "Plate, Ludwig Hermann," in *Dictionary of Scientific Biography*, ed. Charles C. Gillispie (New York: Charles Scribner's Sons, 1975); Heinz Penzlin, ed., *Geschichte der Zoologie in Jena nach Haeckel (1909-1974)* (Jena and Stuttgart: Gustav Fischer, 1994).

27. August Pauly, *Darwinismus und Lamarckismus: Entwurf einer psychophysischen Teleologie* (Munich: Ernst Reinhardt, 1905); Oskar Prochnow, "Mein Psychovitalismus," *Archiv für Rassen- und Gesellschafts-Biologie* 6 (1909): 232–236.

28. Ludwig Plate, "Gegen den Psychovitalismus: Nachwort zu dem vorste-

Similarly, orthogenetic theories, invoking an inner drive to perfection or any other driving force that was blind to environmental change, also drew fire from Plate. He called them teleological, vitalistic or mystical because of the internal causes of change that they posited, and he pointed out that any number of other theories, from Theodor Eimer's environmental effects to natural selection to Weismann's germinal selection, could account for evolutionary trends just as well. Plate had no patience with paleontologists who arranged fossil specimens into neat, progressive lines and thought that that would suffice to prove directed change. When O. Jaeckel did just that, Plate responded severely and condescendingly and reduced him to sputtering about his years of experience with fossils and Plate's lack of respect.[29] Plate continued to make an example of him in later editions of his book.[30]

Richard Semon

Haeckel's student Richard Semon responded to different sorts of challenges to the primacy of external causes. He supplied crucial details of how the internal in-

henden Aufsatze von O. Prochnow: 'Mein Psychovitalismus,'" *Archiv für Rassen- und Gesellschafts-Biologie* 6 (1909): 237–239.

29. Otto Jaeckel, "Erwiderung auf Herrn Plate's Kritik meines Aufsatzes über Descendenz," *Naturwissenschaftliche Wochenschrift* 18 [= NF 2] (1902): 234–235; Ludwig Plate, "Ueber O. Jaeckel's Schrift betreffend die verschiedenen Wege phylogenetischer Entwicklung," *Naturwissenschaftliche Wochenschrift* 18 [= NF 2] (1902): 101–3.

30. Plate, *Selektionsprinzip*, see n. **??**, 502 & 512.

teracted with the external in his 1904 *Mneme* theory of heredity as an analogue of memory. Semon's dedication to the Haeckelian program was evident throughout the book. His concept of organic memory was strictly monistic, in the Haeckelian sense, in that no conscious mind or non-material spirit was involved. The protoplasmic material stored environmental effects as "engrams" and recalled and replayed—or, in Semon's elaborate terminology, "ekphorized"—them to make the embryo repeat the ancestral changes at appropriate times in its development.[31] In subsequent editions he worked out his arguments against Mendelism and experimental embryology, which were threatening the Haeckelian balance between the internal and the external.

Organic memory provided the continuity of substance and form, back to distant ancestors, but there were also provisions for external stimuli to throw the historical pattern off course, introducing novelties, which would in turn be stored in the protoplasm and possibly replayed in future embryos. This dual mechanism of internal storage and replay of old protoplasmic responses and external stimulation of new ones provided a renewed justification of Haeckel's program of reconstructing phylogeny from embryonic evidence,[32] while advancing Haeckel's monistic goal of unifying mental and physical processes. It also underscored what Haeckel had said about the uniqueness of every individual. Not only did

31. Richard Semon, *Die Mneme als erhaltendes Prinzip im Wechsel des organischen Geschehens*, 1st ed. (Leipzig: Wilhelm Engelmann, 1904).

32. Richard Semon, *Die Mneme als erhaltendes Prinzip im Wechsel des organischen Geschehens*, 2nd ed. (Leipzig: Wilhelm Engelmann, 1908), 22 & 383-4.

every individual experience and respond to the environment in its own way, its protoplasm also carried a unique *Mneme* or complement of stored memories of its ancestors' experiences of and responses to the environment.

The principle of individual uniqueness, together with the doctrine of external causes, were at the heart of Semon's answer to the challenges of the twentieth century that Haeckel had been ignoring. *Entwicklungsmechanik*, Semon argued, was misguided as long as it concerned itself exclusively with the inner causes of change. The experimental embryologist reasoned that the fusion of the sperm and egg nuclei determined the outcome of the first cleavage division; that the position of each daughter cell in the early embryo then caused it to divide and differentiate in a certain way; and that the subsequent development of each organ was determined by further differences in the internal environment. But, according to Semon, that sequence of internal causes and effects was only half the story. Internal stimuli within the embryo did not determine the course of development by themselves, the mnemic constitution of the embryo's protoplasm mattered, too. Here we see Semon supplying further detail to support Plate's claim, contra Wasmann, that every individual had a unique constitution and would therefore respond uniquely to an environmental stimulus. The unique constitution was a product of historical events, as "remembered" by the protoplasm.[33]

Since every individual had a unique complement of engrams, it was an illusion to think one could perform repeatable experiments and ignore phylogeny as a cause of ontogeny. *Entwicklungsmechanik*, and experimental methodology

33. Ibid., 229-253.

generally, were invalid because they treated all individuals as interchangeable, ignoring their varied histories and complements of ancestral memories. It was therefore unsafe to generalize from biological experiments or to assume that the experimental treatment alone was the cause of the experimental outcome. In the 1908 edition of his Semon extended this reasoning to Mendelian genetics. The Mendelians, too, failed to ask about the histories of their experimental specimens and viewed them as interchangeable, just because they shared a particular characteristic.

For Semon, Mendelian phenomena such as segregation or dominance were merely special cases of developmental plasticity, which he explained as follows: Imagine hearing two different versions of a line by Goethe, which differed only at the end. If the beginning of the line is then read aloud as a stimulus, which ending should ekphorize and spring to mind? Depending on the circumstances, it might be either one. Similarly, depending on the engraphically recorded history of its lineage, an embryo could have two or more engrams available for ekphorizing at any given point in development. Such dichotomies or branching points accounted for differences between the sexes, between castes of bees and ants (i. e., workers, queens, drones) and other kinds of variation within a species.[34]

These branching points also made Semon's system into a full-fledged alternative to Mendelian genetics. If one hereditary trait appeared to be "dominant" over another, all that meant was that one of two engrams was consistently

34. Ibid.

ekphorized in the hybrid. If the recessive trait reappeared in the offspring of the hybrid, that was the result of a developmental branching that favored the other engram in some of the offspring. He could even explain the characteristic Mendelian ratios by assigning an equal probability of ekphorization to every engram at a given branching point, just as the Mendelians assigned equal probabilities to alleles for a given trait. Semon argued that one should not accept the Mendelian model of genes located on chromosomes and dictating heredity just because it made the correct quantitative predictions. His memory analogy could do the same.[35]

Paul Kammerer as a Monist

Paul Kammerer is not remembered primarily for his monism, but for his efforts to produce experimental demonstrations of the inheritance of acquired characteristics, the accusations of fraud leveled against him, and his dramatic suicide in 1926.[36] But Kammerer's zeal for the inheritance of acquired characteristics was rooted in a conception of Darwinism very close to Haeckel's, in which variation

35. Ibid., 297-325, 333-345.

36. Lester R. Aronson, "The case of The Case of the Midwife Toad," *Behavior Genetics* 5 (1975): 115–125; Sander Gliboff, "The case of Paul Kammerer: Evolution and experimentation in the early twentieth century," *Journal of the History of Biology* 39 (2006): 525–563; Albrecht Hirschmüller, "Paul Kammerer und die Vererbung erworbener Eigenschaften," *Medizinhistorisches Journal* 26 (1991): 26–77; Arthur Koestler, *The Case of the Midwife Toad* (New York: Random House, 1971).

and evolutionary progress were driven by environmental effects, as well as in monistic ideals.

Kammerer aspired to inherit Haeckel's mantle as the leading German-language popularizer of Darwinism and proselytizer for a materialistic view of life and a biological basis for ethics and politics. With feigned modesty, Kammerer once described himself as a mere pebble compared to the planet-sized presence and legacy of an Ernst Haeckel, but he added that he was a very special pebble. With the aid of Haeckel's gravitational influence, he felt he could be the one to start a landslide and change the face of the globe.[37] To that end, Kammerer devoted a great deal of effort to public lectures, adult education, and popular writing, linking specific points of heredity and evolutionary theory to social, political, and religious implications. Kammerer's essays in Monist publications made especially strong connections between Haeckel's older program and Kammerer's modernized goals and theories.

Kammerer's devotion to Haeckel, though heartfelt, was far from blind, however. On some political and social issues, the two were quite far apart. Kammerer's socialist leanings and pacifism contrasted sharply with Haeckel's liberal nationalism and support for the First World War, and he did not shy away from confrontation with other monists over biological arguments for nationalism and belief in German racial superiority.[38]

37. Paul Kammerer, "Haeckel und ich: Der Planet und der Kieselstein," in *Was wir Ernst Haeckel verdanken: Ein Buch der Verehrung und Dankbarkeit*, ed. Heinrich Schmidt (Leipzig: Unesma, 1914).

38. Paul Kammerer, "Nationalismus und Biologie," *Das monistische*

Still, Kammerer and Haeckel were close together on fundamental points. Kammerer came out strongly in support of Haeckel recapitulationism and against *Entwicklungsmechanik* and newer interpretations of embryology.[39] He elaborated on Haeckel's principle of the unity of mental and material phenomena and the notion of the cell as the fundamental unit of body as well as mind.[40] And he attacked August Weismann's germplasm for trying to overturn Haeckel's monistic-mechanistic solution to the problem of variation.[41] He put a modern gloss on Haeckel's doctrines by illustrating them with examples from his own experiments and field studies, applying them to current issues in genetics and eugenics, and arguing that they were the biological theories best compatible with monism and cultural progress. Two essays from 1912 and 1913, on heredity, illustrate Kammerer's monism particularly well.

In "Monistische und dualistische Vererbungslehre" [Monistic and dualistic hereditary theory],[42] Kammerer applied Haeckel's distinction between the roles

Jahrhundert: *Wochenschrift für wissenschaftliche Weltanschauung und Weltgestaltung* 2, no. 42 (1914): 1177–1185.

39. Paul Kammerer, "Das biogenetische Grundgesetz," *Das monistische Jahrhundert*: *Wochenschrift für wissenschaftliche Weltanschauung und Weltgestaltung* 1/2, no. 22 (1913): 721–727.

40. Paul Kammerer, "Gefühl und Verstand," *Monatsblätter des Deutschen Monistenbundes, Ortsgruppe Hamburg*, April/Mai 1914, from a photocopy in the Kammerer Papers, American Philosophical Library, Philadelphia.

41. Paul Kammerer, "Körperplasma und Keimplasma," *Das monistische Jahrhundert*: *Wochenschrift für wissenschaftliche Weltanschauung und Weltgestaltung* 2, no. 29 (1913): 668–677.

42. Paul Kammerer, "Monistische und dualistische Vererbungslehre," *Das monistische Jahrhundert*: *Wochenschrift für wissenschaftliche Weltanschauung*

of internal and external causes of change. His main targets were August Weismann, for isolating the immortal, hereditary germplasm from environmental influences, and various Mendelians, for similarly denying the importance of the environment in inducing evolutionary change. Kammerer appealed to monist assumptions about the unity of all substance to show that the Weismannian distinction between germplasm and somatoplasm was counterintuitive, unnatural, and "dualistic," a term which his readers would take to mean not only belief in two biological substances, but in a non-material spirit world. Kammerer disparaged "the idea that there could be parts in an organism [i.e., like the isolated germplasm] that have nothing to do with the good or ill of the rest. . . ." and he compared the germplasm to a parasite:

> In the same way that, for example, no attributes of the human form are transferred to the tapeworm just because it lies in the human bowels, just as little of the personal experiences of the individual are conveyed to the germplasm that is nourished by him and is in a certain way parasitic on the germ-bearing body.[43]

Kammerer's main objection to the idea of a separate germplasm was that there was no apparent way for the evolutionary process to produce truly novel, creative changes in it. Echoing Haeckel, and addressing Weismann's theory more specifically than Haeckel had ever done, Kammerer criticized Weismann

und Weltgestaltung 1, pt. 1, no. 7 (July 1, 1912): 225–235.

43. Ibid., 226.

for isolating the germplasm completely from environmental effects and indeed from just about any imaginable causes of change.[44] By Kammerer's reading, the "determinants," the elementary hereditary units in the Weismannian germplasm, did not change at all. Variation arose only by means of sexual reproduction, which "continually made new combinations out of a permanently given stock of characteristics."[45]

This meant, according to Kammerer, that all heritable characteristics were "contained in the germ from the beginning." Sexual reproduction could bring old traits together in new combinations, and selection could eliminate some of them, but that was all. There was no provision for true novelty:

> Something new can only arise through selection, which can only eradicate the non-useful characteristics and accumulate the useful—as well as through crossing, which continually makes new combinations out of the supply of characteristics that is given once and for all.[46]

44. This is perhaps unfair, because by the time of Kammerer's writing, Weismann had actually given several different accounts of whether or how the germplasm could be modified. Kammerer was evidently holding him to the version from: August Weismann, *Die Bedeutung der sexuellen Fortpflanzung für die Selections-Theorie* (Jena: Gustav Fischer, 1886). On the evolution of Weismann's views on the causes of variation, see Rasmus G. Winther, "August Weismann on Germ-Plasm Variation," *Journal of the History of Biology* (2001).

45. Kammerer, "Monistische und dualistische Vererbungslehre," see n. **??**, 225-226.

46. Ibid., 226-227.

For Kammerer, the immortal and unchanging determinants therefore represented a revival of preformationism, in which evolution could only work out the lineage's pre-existing potential, and from preformationism it was but a small step to creationism.

Kammerer included standard interpretations of Mendelism, especially the saltational ones, in the same dualist-preformationist-creationist category as Weismann's germplasm theory. He called them all veiled throwbacks to archaic belief in the fixity of species, "because [they] implied a doctrine of, if not absolute, then relative *immutability of plant- and animal species.*" [Emphasis original]. Such a theory was not only false, but incomplete and intellectually unsatisfying:

> The inquisitive mind, searching for causes, will feel most of all unsatisfied because the *very first appearance* of those myriad traits ("determinants"), of which it is asserted over and over that they were always present in the germ, remains in the dark.[47]

Most of the essay was devoted to freeing Mendelian genetics of Weismannian influences. What the theory needed, according to Kammerer, was a properly scientific and monistic account of genetic change, that is, of the causes of mutations. He accused geneticists of treating mutations as random or spontaneous and uncaused, which was unscientific and unacceptable to a monist:

47. Ibid., 227, emphasis original.

> It is no coincidence that modern geneticists, Mendelians, and Mutation theorists are mostly also dualists: vitalists and psychists, who consider life to stand outside the realm of natural causality. The proponents of the monistic theory of heredity, in contrast, are mechanists, energeticists.[48]

Kammerer's solution to the problem of mutation was Haeckel's doctrine of external causes. Even though he could not pinpoint the causes of mutation any better than his opponents, he knew there must be a materialistic and externalistic explanation. The hereditary material must be shaken up somehow, by environmental influences. He cited his own experiments as evidence that the environmental could alter an organism's heredity, and he argued that there was no difference, in principle, between the continuous changes he produced in the laboratory and the more discrete changes that are classified as mutations.

Last, but not least, Kammerer argued that the Weismannian view of Mendelism had to be rejected because of its social and political consequences. He made a case for the inheritance of acquired characteristics as the basis for and justification of universal education and public health measures, and contrasted it with the ruthlessness of selectionist eugenics: "The reactionaries in science and politics reach out over the doctrine of the non-heritability of acquired characteristics to shake each other's hands."[49] Indeed, Kammerer spent many years promoting an elaborate program for social, cultural, moral, and medical progress, based on the

48. Ibid., 229.

49. Ibid., 231.

premise that the beneficial effects of medication, nutrition, education, and practice could be made hereditary,[50] and these monistic essays show how strongly his social views and plans were rooted in Haeckel's monism and teachings about external causes of change.

Conclusion

Monism was more than just an philosophical flourish in Haeckel's biology. It was part and parcel of a conception of biology as a mechanistic, historical, and a-teleological science, and it provided criteria for demarcation between science and religion, along with constraints on the allowable causes of evolutionary change. Hence, monism entered into conceptions of the mechanisms of variation and natural selection and was a central motivation in turn-of-the-twentieth-century debates over evolution.

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50. Sander Gliboff, "'Protoplasm…is soft wax in our hands': Paul Kammerer and the art of animal transformation," *Endeavour* 29 (2005): 162–165.

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