

## HISTORY OF SCIENCE

## An Alternative Synthesis

Ron Amundson

**F**rom *Embryology to Evo-Devo* presents a collection of papers by historians, philosophers, and biologists that were discussed at a Dibner Institute workshop in the fall of 2002. It immediately brings to mind a similar work, *The Evolutionary Synthesis (1)*. This pair of edited volumes, appearing a quarter-century apart, offers an almost yin and yang of the history of evolutionary thought. Most 19th-century evolutionists saw embryonic development as central to the evolutionary process. The contributors to the 1980 volume edited by Ernst Mayr and William Provine viewed it as essentially irrelevant. (Although, as the newer volume shows, many strands of developmental evolutionary thought persisted during the heyday of the modern synthesis.) Evo-devo brings the developmental view of evolution back to the fore.

The only author to appear in both volumes is historian Frederick Churchill. In 1980, he reported a crucial fact about 19th century biology: “Heredity” was then understood as an aspect of embryonic development itself. It was the process by which similar traits developed within both parents and offspring. Evolution obviously involves heredity, and so the interweaving of development and heredity implied an interweaving of development and evolution. The conceptual separation of heredity from development was achieved by T. H. Morgan and his associates. Transmission genetics became the new “heredity,” carved free of development. Only then was evolution easily conceived as independent of development. Churchill claimed that the separation of development from heredity was “fundamental to the formation of modern biology.” It certainly was fundamental to the evolutionary synthesis. Transmission genetics begat population genetics, which begat the modern synthesis. At no step along the way was development relevant to evolutionary change (2). Most contributors to Mayr and Provine described the then-60-year history of the evolutionary synthesis as utterly separate from

embryology and from related fields, such as comparative morphology and versions of systematics that emphasized higher taxa.

In the 2007 volume, edited by Manfred

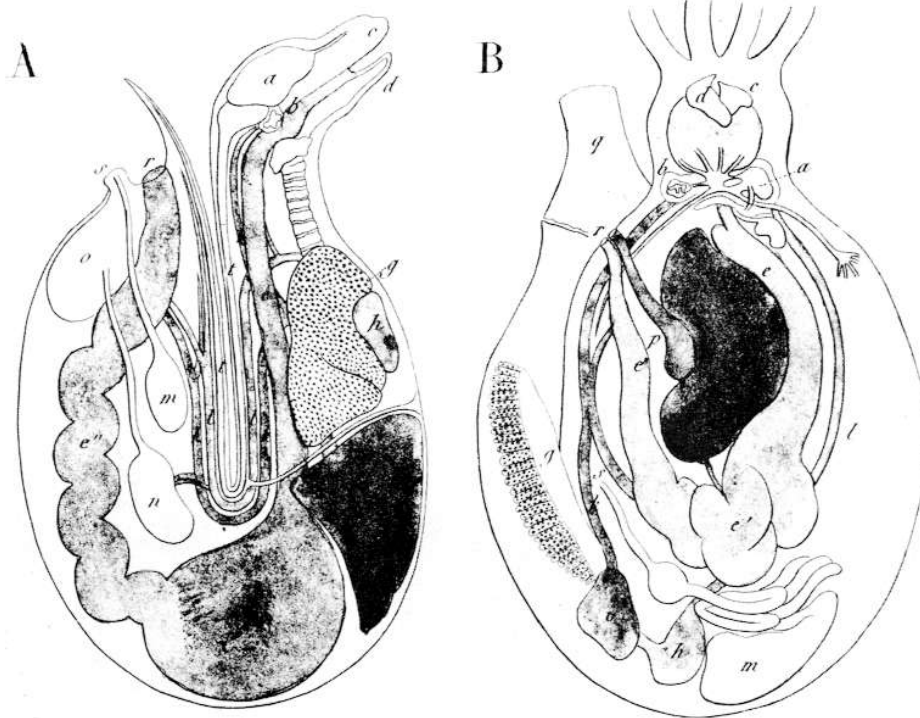
Laubichler and Jane Maienschein, Churchill takes a subtly different stance toward the bifurcation of development and heredity. He discusses the refutation of the biogenetic law by 19th-century contemporaries of Ernst Haeckel. The results were the research programs in evolutionary embryology

of such figures as Francis Balfour, Eugen Korschelt, and Karl Heider. These biologists took account of embryonic causation and adaptation, not only the appearances of recapitulation. Churchill observes that their programs show many similarities with evo-devo. This theme is taken up many times in the Laubichler and Maienschein volume. Some

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chapters address relations among research traditions: for example, Scott Gilbert discusses fate mapping, cell lineage studies, and the relation of these fields to modern gene expression maps. Other chapters focus on individual researchers, either from before the synthesis (e.g., Balfour and William Bateson) or from the era in the 20th century when it held sway (e.g., Dwight Davis, John Tyler Bonner, and Rupert Riedl).

I couldn't help but wonder where this new perspective leaves the bifurcation of heredity from development. If evo-devo turns out to be the success that its advocates are envisioning, perhaps we will witness a breakdown of the heredity-development dichotomy. Recent discussions of what is now called “epigenetics”—a field that centers on development—have come very close to saying that it simultaneously involves heredity (3). Philosopher James Griesemer's chapter addresses this issue, beginning with Gregor Mendel and August Weismann. These are the two 19th-century heredity theorists usually thought to be most “modern,” in the Churchillian (1980) sense of conscientiously separating heredity from development. According to Griesemer, this is an error. Mendel and Weismann shared the assumptions of their contemporaries; heredity was an aspect of development. He goes on to argue that transmission genetics



**Differ by inversion?** Étienne Geoffroy Saint-Hilaire claimed that all animals share a fundamental body plan and suggested a dorsoventral inversion between vertebrates and invertebrates. To ridicule such comparisons among body plans, Georges Cuvier drew roughly comparable arrangements of organs in a duck folded on its back (A) and a cephalopod (B). He argued that there are far more differences than similarities [from (5)].

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itself is a study of development. It must be the study of development in the sense that the study of cooking “must be” the study of chemistry. (Chefs may deny that they are studying chemistry, but chemists know better.)

One underlying message of many of the chapters is that historical attempts to explain evolution in terms of development were productive but incomplete (contra *The Evolutionary Synthesis*). Evo-devo is a promise for their completion. (The historians tended to avoid this presentist bias, but philosophers and scientists found it nearly irresistible.)

One weakness in the presumption of continuity between historical theorists and modern evo-devo is the current prominence of the comparative molecular mapping of gene expression. That field is crucial to evo-devo. As Gilbert’s chapter points out, it “brought the notion of structure back into developmental biology.” Without the centrality of organic structure, any similarities between the centuries are superficial. But as informative as it is, gene expression mapping is analogous only to a narrow range of historical precursors, comparative embryology and morphology (scarcely more than what Ernst Haeckel considered). These fields do not yield mechanistic explanations of evolutionary change. If evo-devo is to fulfill its promise, it must go beyond comparison and provide causal details of the actual changes in ontogeny by which new forms were evolved.

Such causal details are often claimed to be viable goals for evo-devo explanations of evolutionary innovations and novelties (discussed in the chapters by Alan Love, Gerd Müller, and Günter Wagner). What we now call innovation and novelty was previously studied under the rubric of “origins of higher taxa”: such as the neural crest characterizing vertebrates and the fin-limb transition for tetrapods. Some argue that evo-devo has greater potential to explain novelties than the modern synthesis had because population genetics can only deal with modifications of structures that already exist (e.g., in terms of preadaptation). Evo-devo has theoretical access to the causal processes of embryogenesis, which can potentially explain the origins of genuinely novel structures. Innovations are not merely modifications of old structures, but new products of modified ontogenies.

However, Wagner cautions against too much optimism. He recalls the breakdown of evolutionary embryology around the turn of the 20th century. Its advocates had expected to solve the evolutionary problem of form by studying comparative morphology and

embryology (with a bit of experimental embryology thrown in). But practitioners could not agree on methodology. The relative importances of embryological and adult morphologies, embryonic adaptations, and causal processes within the embryo were all at issue. The field reached a stalemate by the early 20th century. Wagner believes that evo-devo might suffer the same fate.

But won’t molecular biology save us from that fate? Maybe, maybe not. Do we have a principled way of deciding whether the large differences in Hox gene organization between major groups point toward an ancient saltationist cause of evolutionary change (in duplications of Hox clusters, for example) or reflect a later built-up by-product of gradual micro-evolutionary changes (4)? Wagner argues that we may never be able to know the genuine mechanisms by which ontogenetic changes occurred; they may have been too ephemeral

to have left evidence. If this is the case, evo-devo will not fulfill the promise of its 19th-century precursors but instead recapitulate their failures.

But it hasn’t so far. Like all good history, the studies in *From Embryology to Evo-Devo* give a perspective on the present as well as the past. The same is true when we reread *The Evolutionary Synthesis*.

#### References

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## PHYSICS

# Relativists, Skepticism, and Waves

Michael D. Gordin

Gravitational waves are simultaneously a hot topic and a matter of no interest. On the one hand, the U.S. National Science Foundation (among others) has paid out enormous funds for the Laser Interferometer Gravitational-Wave Observatory (LIGO), which is expected to provide the first concrete evidence of the existence of these waves coursing across the fabric of space-time. You don’t get that kind of funding unless there is something to be found and that something is quite important. On the other hand, essentially nobody doubts the outcome of LIGO’s work.

Although they have never been unambiguously detected, gravitational waves are simply assumed to exist—they are now seen as required by Albert Einstein’s general theory of relativity—and LIGO will only put the icing on a cake physicists consumed a long time ago.

Or so one would think, talking to contempo-

rary gravitational physicists (often called “relativists,” without the rancor scientists direct toward historians of that stripe). The great achievement of Daniel Kennefick’s fascinating *Traveling at the Speed of Thought* is that he takes this assumed existence of gravitational waves apart. He is not out to show that they do not exist—far from it. Rather, he carefully explains how durable skepticism has been toward the existence of gravitational waves ever since Einstein first predicted them in 1916. Even Einstein was a sometime skeptic, and many of his direct collaborators maintained severe doubts after his death. Yet gravitational waves are now taken for granted. Kennefick tells us how this common sense emerged.

This is no mean feat, considering how complicated the physics of general relativity is, and how hard it is to perform the calculations that predict the existence and behavior of the astonishingly weak gravitational waves. To one extent, then, Kennefick offers a readable (although at times overly technical) account of the theory of gravitational waves, exploring why skepticism was a reasonable stance at various points in the 20th century and why it has ceased to be so in the 21st. This eminently interesting account is, however, the less intriguing aspect of Kennefick’s book.

The more interesting aspect concerns the role of analogy in science. Gravitational waves

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