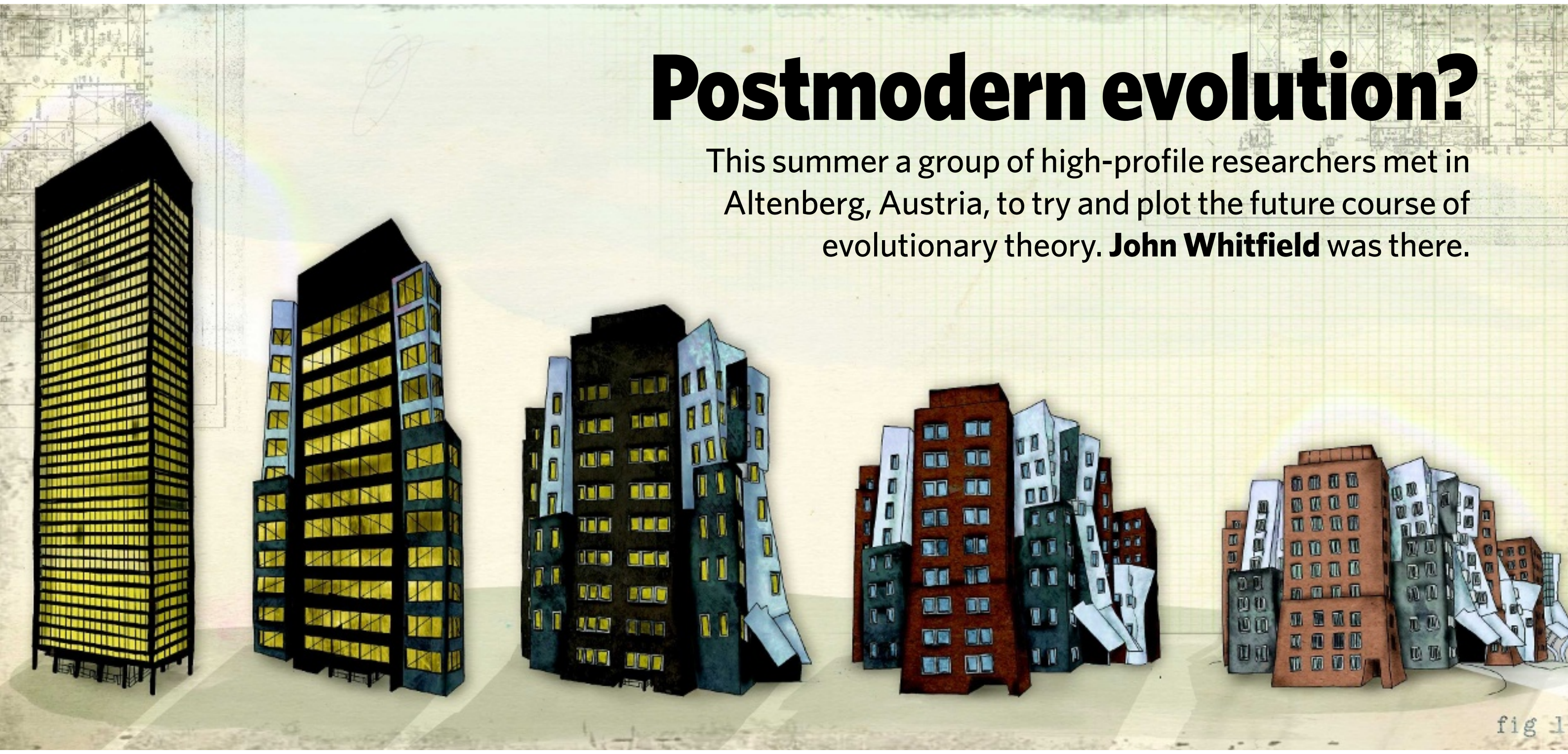


Postmodern evolution?

This summer a group of high-profile researchers met in Altenberg, Austria, to try and plot the future course of evolutionary theory. **John Whitfield** was there.

ILLUSTRATION BY J. TAYLOR

"Oh my gosh," says Massimo Pigliucci, "maybe I shouldn't use that term." Pigliucci, responding to comments on his talk about how living things respond to their environment, and what it means for evolution, has just let slip the p-word. Later the same day, Günter Wagner, an evolutionary theorist at Yale University in New Haven, Connecticut, puts up a slide bearing the words 'Postmodern Synthesis'. Pigliucci is moved to make an editorial suggestion from the floor: "I'd really rather we didn't use that term." Wagner says the slide was intended to be tongue-in-cheek, but Pigliucci is worried about the impression the word creates: "If there's one thing we don't want, it's for people to get the idea that there's a bunch of evolutionary theories out there, and that they're all equal."

A lot of scientists loathe what they take to be postmodernism's intellectual relativism, and shy away from using the word. But doing so puts Pigliucci in something of a bind. An evolutionary ecologist at the State University of New York in Stony Brook, Pigliucci is one of the conveners of this small meeting on the future of evolutionary thought taking place at the Konrad Lorenz Institute for Evolution and Cognition Research in Altenberg, Austria. The meeting has received a fair amount of hype — in the blogosphere it was dubbed 'The Woodstock of Evolution'. Its agenda is, pretty explicitly, to go beyond the 'modern synthesis' that has held sway in evolutionary theory since the middle of the twentieth century. And in everyday speech, it is pretty clear what comes after the modern.

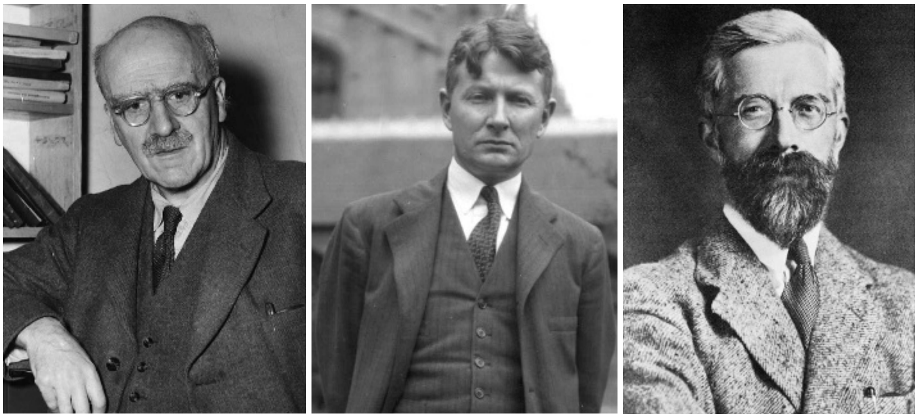
What's more, some of this work sounds as though it fits the term quite nicely. Over dinner at the meeting's end, Pigliucci expresses his hope of "moving from a gene-centric view of causality in evolution to a pluralist, multi-level causality". Postmodernists in the humanities call this 'decentering', and they are all for it. Over the course of the meeting, it's fairly clear that the means to this pluralist end are being sought through mixing and matching neglected ideas and old problems from biology's past with the latest experimental and analytical techniques. Apply that sort of bricolage to architecture and you get the sort of brutalist-right-angle here, classical-column-there, swirling-titanium-ceiling-above-it-all look that is normally pigeonholed, for better or worse, as postmodern.

> **"The modern synthesis is good at modelling the survival of the fittest, but not the arrival of the fittest."** — Scott Gilbert

Evolution of ideas

Leaving aside the troublesome adjective, what is the modernism that the Altenburg meeting is meant to move beyond — or to use Pigliucci's preferred term, 'extend'[1]? Between about 1920 and 1940, researchers such as the American Sewall Wright and the Englishmen Ronald Fisher and J. B. S. Haldane took Charles Darwin's ideas about natural selection and Gregor Mendel's insights into how traits pass from parents to offspring — which many biologists of the time believed antithetical — and fused them into a mathematical description of the genetic makeup of populations and how it changes. That fusion was the modern synthesis. It treats an organism's form, or phenotype, as a readout of its hereditary information, or genotype. Change is explained as one version of a gene being replaced by another. Natural selection acts by changing the frequency of genes in the next generation according to the fitness of phenotypes in this one. In this world view, the gene is a black box, its relationship to phenotype is a one-way street, and the environment, both cellular and external, is a selective filter imposed on the readout of the genes, rather than something that can influence an organism's form directly.

What's wrong with this picture, say the would-be extenders at Altenberg and elsewhere, is what it leaves out. Molecular biology, cell biology and genomics have provided a much richer picture of how genotypes make phenotypes. The extenders claim that enough insights have now come from this and other research for it to be time to re-examine problems that the modern synthesis doesn't address. These problems include some of the key turning



Modern synthesists: (left to right) J. B. S. Haldane, Sewall Wright and Ronald Fischer.

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points in evolution: the patterns and changes seen in the fossil record as new branches spring from the tree of life and new anatomies — skeletons, limbs, brains — come into being. "When the public thinks about evolution, they think about the origin of wings and the invasion of the land," says Graham Budd, a palaeobiologist at the University of Uppsala, Sweden. "But these are things that evolutionary theory has told us little about."

Bring on the kangaroos

The question of how form changes in individuals is the province of developmental biology, and genetic studies have now revealed a lot about how the mechanisms of development have evolved. Many see the evolutionary developmental biology — 'evo-devo' — that is emerging from this work as the key ingredient needed to extend or surpass the modern synthesis.

"Evolution needs a theory of body construction and change, as well as population construction and change," says Scott Gilbert, an evo-devo researcher at Swarthmore College in Pennsylvania, who was not in Altenberg but who is writing a book on extending the evolutionary synthesis in similar directions. "The modern synthesis is remarkably good at modelling the survival of the fittest, but not good at modelling the arrival of the fittest." To explain the production of novel features, such as limbs and feathers, Gilbert and like-minded biologists want a theory in which the environment is defined broadly enough to include the developing body, which is the primary context in which the genes are expressed. Genes shape this developing environment, but the dynamic environment also shapes the expression of the genes. And it does so directly, rather than through some later selection. "The gene will continue to be centre stage," says Gilbert, "but it will be seen as both active and acted upon. It's not going to be the unmoved mover."

The importance of the environment acting on the genome can be seen in plasticity, the ability of the same genes to give rise to radically different phenotypes in different conditions — as studied by several of the Altenberg group. Pigliucci, who works on invasive plant species, gave the example of species that lie low in a new environment for several years before becoming a problem. He puts this down to plasticity and the Baldwin effect. In 1896 James Baldwin, an American psychologist, suggested that over the generations, tricks that at first have to be learned can become hard-wired as genes fix variations caused by the environment. "It could be that the plants arrive in a new environment and hang on thanks to plasticity — it gains time for natural selection to kick in," says Pigliucci. To begin with, the genes follow adaptation rather than leading it, as "bookkeepers of what's happening". Once the genes have caught up, and the immigrant can take adaptation to the environment as read, it is able to become dominant.

Plasticity also allows organisms to make the most of their mutations. "The myopic view — that we don't need to worry about phenotypic variation, that it is abundant, always small and that it goes in all possible directions — doesn't correspond to the conservation we've seen in developmental systems," Marc Kirschner, a systems biologist at Harvard University in Cambridge, Massachusetts, told the Altenberg meeting. To grow a limb you don't need mutations in every gene involved in limb building; life can use the facts that muscle cells naturally align with bone, nerve cells stabilize when they plug into muscles, and blood vessels grow towards areas low in oxygen to leverage a small genetic change into an important difference. Again, the changing environment within the developing body is part of the process by which the gene is expressed: Kirschner calls it facilitated variation[2].

As an example, he points to the discovery that the narrow, tweezer-like beak of an insect-eating finch can become the fat, nutcracking beak of a seed-eater by increasing the activity of a single gene involved in bone formation[3]. "Because developmental systems are so integrated and self-regulating, you can make a large functional change without a large genetic change," says Kirschner. Pigliucci gave a more speculative example of the possible evolutionary consequences of such changes, showing a slide juxtaposing a kangaroo and a dog that had been born without forelimbs but learnt to walk on its hind legs. "It's hard to imagine that this kind of change doesn't have anything to do with the evolution of bipedalism," he told the meeting.

Self-organizing cells

Pigliucci and Kirschner think that the capacity of small genetic changes to trigger large shifts results in waves of innovation separated by seeming lulls in which evolution stablizes and integrates the new arrangements. This matches some aspects of the fossil record, where bursts of innovation and diversification are interspersed by much longer periods of stasis — a pattern known as punctuated equilibrium, first described by the late Stephen Jay Gould and Niles Eldredge of the American Museum of Natural History in the 1970s. Gilbert, who studies turtles, sees something similar: "Turtle biologists joke that one Tuesday in the late Triassic there weren't any turtles, and by the weekend the world was full of turtles. One reason why might be that it's not all that hard to make a shell — all the genes are probably there already, and it doesn't take many changes to get a shell."

"Our way of looking at evolution counters genetic determinism and its political implications." — Eva Jablonka

Stuart Newman, a developmental biologist at New York Medical College, takes such ideas further than most, arguing that the abilities that cells have to self-organize into complex structures can lead to major evolutionary innovations such as the origin of the vertebrate limb — a problem on which he collaborates with Altenberg's other organizer, evo-devo researcher Gerd Muller of the University of Vienna, Austria[4] — with

B. LORENZ/KLI

The Altenberg Sixteen at the Konrad Lorenz Institute for Evolution and Cognition Research.

perhaps little or no genetic change. "You can't deny the force of selection in genetic evolution," says Newman, "but in my view this is stabilizing and fine-tuning forms that originate due to other processes."

The same process might have given rise to animals themselves. The further you turn back the clock through geological time, Newman believes, the weaker genetic regulation of development becomes relative to plasticity and self-organization. The development of the most basic features of multicellular organisms some 600 million years ago, in the late Proterozoic, might have been the rapid and spontaneous result of molecules already present on unicellular organisms doing new jobs when cells stick together[5]. "You don't need incremental change under gradual selection regimes to get attributes such as segmented, hollow or multilayered bodies," says Newman. "You can get it all with thermodynamics and self-organization."

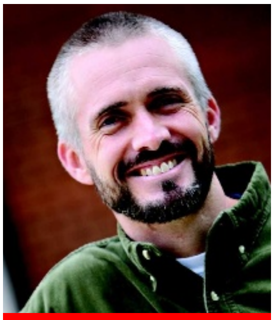
The problem is testing such ideas. Newman suggests that knocking out the genes that stabilize development in model laboratory organisms might provide insights, but extrapolating back from modern organisms to their distant ancestors is fraught with problems. It is difficult to see how such an approach can get beyond the theoretical, says Budd, adding that what evidence there is weighs against Newman's hypothesis. "Clearly there are physical and chemical processes that affect cells," says Budd. "But I don't think there is any evidence at all for the idea that development was more permissive and plastic [in the Proterozoic] and that body plans could spontaneously emerge. The fossil record shows that body plans appeared sequentially in a series of innovations, not in a misty way at the bottom of the tree."

Confusing what can happen and what did happen is a common criticism of the ideas raised at Altenberg. For example, some lab studies lend support to the Baldwin effect: experiments with fruitflies show that following up an environmental stress with selective breeding can produce animals that show the phenotypic response to that stress without having experienced it[6]. But there is little evidence so far that genetic change in wild populations takes this course, says Wagner. "The idea that environmentally induced changes are the path-breaker for genetic fixation is an old one, but I'm not yet convinced that's how it works in real populations," he says.

"These notions haven't forced us to change the neo-darwinian paradigm," says Jerry Coyne, an evolutionary geneticist at the University of Chicago. Coyne has little time for "evo-devotees"[7] who think that the discipline will cause a revolution in biology. Researchers coming at evolution from population genetics are particularly resistant to any attempt to displace natural selection from the place at the heart of evolutionary theory that the modern synthesis provided it with. "The whole thing about natural selection being an insufficient paradigm seems grossly overblown," says Coyne. "There are a lot of interesting new things coming out that will change our view of evolution. But to say the modern synthesis is incomplete or fatally flawed is fatuous."

And it is worth noting that you can work in evo-devo and not subscribe to such ideas. Sean Carroll of the University of Wisconsin in Madison sees things in terms of bridge-building, not replacement. "What did population genetics and palaeontology have to do with each other for the past 80 years? Nothing. The modern synthesis describes evolution within populations — it's agnostic or silent about the cumulative effect of that process," he says. By revealing the genetic basis of development, and showing how genetics relates to morphology, evo-devo "sits right in the middle" of the two disciplines, says Carroll.

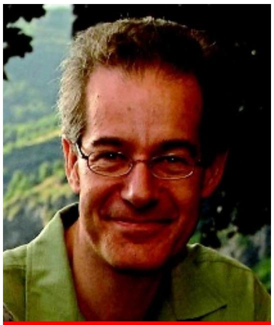
The true message of evo-devo, Carroll says, is that developmental processes have evolved in a way that allows small aspects of form to be tweaked without affecting the whole organism — something which tends to reinforce



K. MACWILLIAMS/UNIVERSITY OF MINNESOTA

"Evo-devo was the synthesis between evolution and development — now it is what needs to be done to get there."
— Alan Love

the modern synthesis's view of evolution as incremental[8]. "Because we can get large effects when we manipulate genes in development, the spectre that these things have happened in history is out there," says Carroll. "But just because we can make freaky-looking animals in one step, I'm unwilling to say that evolution works that way." Wagner and his colleagues have recently shown that altering many genes in mice produces only a small effect[9], countering the idea that most individual genes have such a wide-ranging influence that changing them would be fatal.



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"If there's one thing we don't want, it's that there's a bunch of theories out there, and they're all equal." — Massimo Pigliucci

The differences of opinion suggest that, although evo-devo may once have looked as if it would unify population genetics and development, so far it has done more to give new voice to important problems that had been pushed to the margin — this was a strong note at Altenberg, making the meeting as much about revivalism as revolution. "Originally, the idea was that evo-devo was going to be the synthesis between evolution and development — now it is part of what needs to be done to get there," says Alan Love, a philosopher of science at the University of Minnesota in Minneapolis who attended Altenberg. "There is still a lot of outstanding work to do on fitting the pieces together, but no consensus on how to go about that right now." Nevertheless, he says, that's no cause for alarm. "What is needed is to incorporate empirical findings into the bigger picture. It took populations genetics 25 years to do that and make the modern synthesis. As far as evo-devo goes, I'd say we're smack dab in the middle of that process."

Preaching to the converted?

David Krakauer, an evolutionary theorist at the Santa Fe Institute in New Mexico who was not at Altenberg, agrees. "It's a matter of finally unifying two areas that haven't spoken to one another," he says. "To tackle any modern problem in evolutionary biology, you'll have to use development and the dynamics of the genes that underlie it." He's quite enthusiastic about the possibility of bringing together mathematical theories of pattern formation, of the kind favoured by Newman, and the large body of theory on genetic change between generations used by population geneticists such as Coyne. But at the same time, he can see forces beyond the content of the theories that may keep them apart: "It's not about totally incompatible world views, it's about who holds the torch — who are the legitimate heirs to the Darwinian intellectual estate."

Love saw the Altenberg meeting as an attempt to bridge the divide, but one that, by avoiding conflict (partly through invitations being declined), ended up a little one-sided. "Altenberg was an attempt to pull people together; the hard part was that it didn't pull in people who were less than sympathetic towards one another," he says. "It could have been a much more eraser-throwing meeting, but there is no reward for organizing that — you don't get another grant by trying to get people in the same room, you just have to take time away from the lab or fieldwork."

And there are forces at play beyond jockeying for disciplinary prestige. Never mind what can happen and what did happen. What should happen? It's a fight that evolutionary theory — rooted as it is in a world view shaped by Victorian capitalism — has always found itself dragged into. To give one example, the championing of 'punctuated equilibrium' in the fossil record by Gould and Eldredge was easily construed by participants on both sides of the debate in the 1970s as an attack from the political left — part of a broader rising of hackles at the arrival of sociobiology, selfish genes and the like. Evolutionary ideas and political metaphors still seem to seek each other out — in an extended synthesis, says Gilbert, "the gene will be a much more constitutional monarch, taking instructions from the cell and environment".

Eva Jablonka of the University of Tel Aviv, Israel, is explicit about a political side to her work. She advocates the importance of epigenetic inheritance — traits that can be passed on without changes to DNA sequence. These can be induced by environmental stressors such as temperature, diet or environmental chemicals. Such mechanisms, and insults, may be behind some inherited diseases, she says, in which case we have a responsibility to curb and reverse them. "There are social implications to our approach," says Jablonka. "Our way of looking at heredity and evolution counters genetic determinism and its political implications." Jablonka is one of the Altenberg attendees most comfortable with the term 'postmodern'.

Yet there was no sense at Altenberg of a desire to attack evolutionary theory from the left. Quite the reverse — the dominant political concern was a fear of attack from fundamentalists. As Gould discovered, creationists seize on any hint of splits in evolutionary theory or dissatisfaction with Darwinism. In the past couple of decades, everyone has become keenly aware of this, regardless of their satisfaction or otherwise with the modern synthesis. "You always feel like you're trying to cover your rear," says Love. "If you criticize, it's like handing ammunition to these folks." So don't criticize in a grandstanding way, says Coyne: "People shouldn't suppress their differences to placate creationists, but to suggest that neo-Darwinism has reached some kind of crisis point plays into creationists' hands," he says. It is tempting to say that it's not just genes that express themselves in an environment that responds and reshapes itself around them, feeding back and complicating matters beyond simple cause and effect; the same applies to ideas. And if that seems a bit self-referential — well, that's postmodernism. ■

John Whitfield is the author of *In the Beat of a Heart: Life, Energy, and the Unity of Nature.*

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