

CONTENTS

<i>Foreword</i>	ix
Part I. Introduction: Why Consider Development?	1
1 Nothing in Biology Makes Sense . . . Anymore	3
2 Rodents' Teeth and Raptors' Toes	12
3 How the Turtle Got Its Shell	20
4 Understanding the Debates	38
Part II. How Development Works	49
5 Opening the Black Box	51
6 Five General Principles of Development	72
Part III. The Developmental Bases of Evolutionary Processes	81
7 Developmental Bias	83
8 Plasticity-Led Evolution	100
9 The Causes of Selection	119
10 Inheritance beyond the Gene	144

viii CONTENTS

Part IV. Implications of the Developmental Perspective	171
11 Novelty and Innovation	173
12 The Developmental Origins of Evolvability	189
13 Human Evolvability	206
14 The Structure of Evolutionary Theory	227
<i>Notes</i>	249
<i>References</i>	337
<i>Index</i>	413

1

Nothing in Biology Makes Sense . . . Anymore

Evolutionary biologists have described many remarkable adaptations, but few as curious as the capacity of woodrats from the Mojave Desert in California to feed on creosote bushes.¹ The bushes themselves are impressive, being able to survive for years without water and to flourish by coating themselves with a highly toxic resin that deters almost all herbivores.² Despite this, Mojave Desert woodrats feed almost exclusively on creosote, maintaining healthy bodies while consuming quantities of toxin sufficient to kill most other animals.³ This unusual fare allows the woodrats to exploit a novel dietary niche, largely free from competition (figure 1).

What makes the woodrats particularly fascinating is that their ability to process the creosote relies completely on the detoxifying capability of the bacteria within their guts.⁴ When researchers treated the woodrats with antibiotics that wiped out that bacterial community, the woodrats dramatically lost body mass and began to deteriorate on the creosote diet.⁵ Conversely, when woodrats that don't consume creosote bushes, and would normally be poisoned by it, were inoculated with the microbiota of Mojave woodrats, they thrived on creosote.⁶ Here the *microbiome*—the collective noun for the array of tiny symbionts, including bacteria, archaea, protists, fungi, and viruses, that reside in organisms' bodies—is passed down through the generations by behavioral means, with each cohort acquiring the detoxifying microbes by consuming soil and feces. Experiments found that feeding feces to creosote-naïve woodrats is effective at transmitting the detoxifying bacteria.⁷ Mojave woodrats have exploited this dietary niche for hundreds of years through the stable inheritance of bacteria acquired from the external environment.⁸

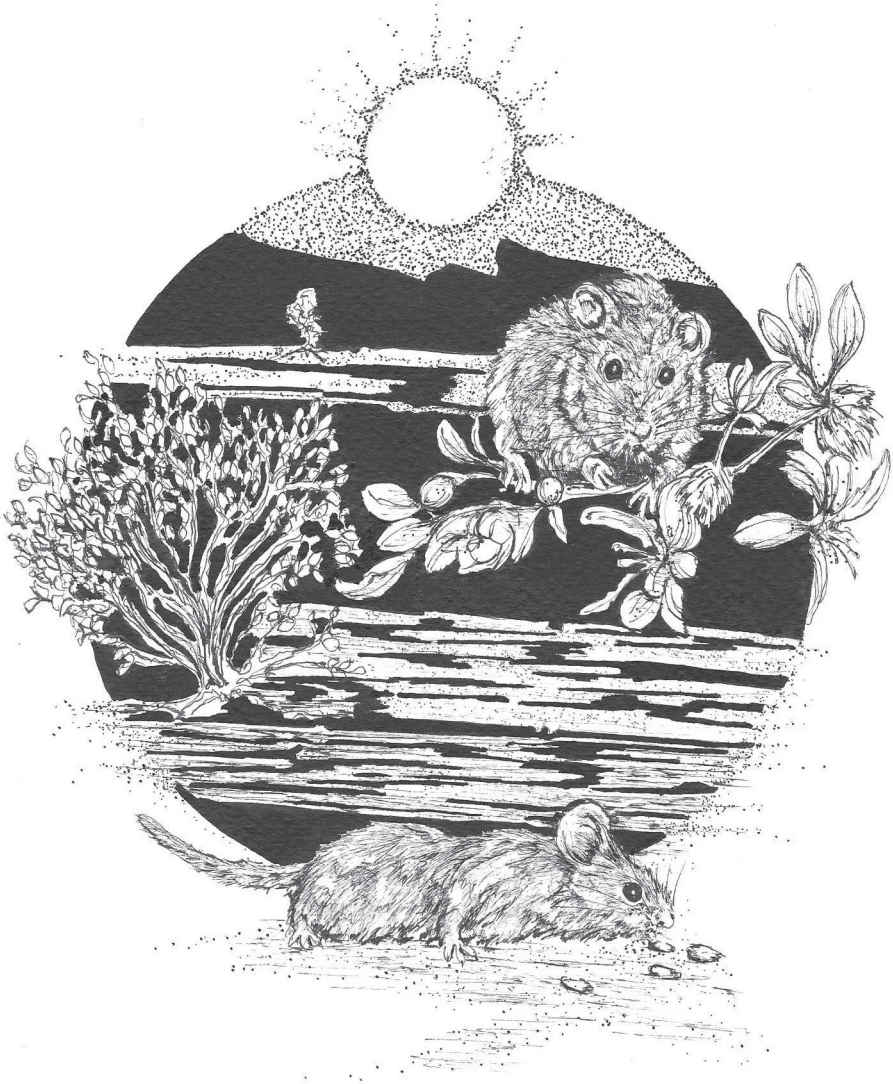


FIGURE 1. Mojave Desert woodrats feed on a toxic diet, thanks to bacteria that they reliably inherit by consuming soil and feces in their environment.

Cross to the other side of America, and just off the east coast a population of humpback whales in the Gulf of Maine has also opened up a new dietary niche. These whales prey on sand lance—an eel-shaped fish that forms large shoals—through an innovative method known as “lobtail feeding”.⁹ This involves a whale thumping the water surface with its tail, which shocks the fish

below into tightening their school, and then the whale spirals around the school releasing air from its blowhole, which traps the fish in a net of bubbles, before it finally lunges up from beneath with its mouth gaping to feast on coral-reef fish.¹⁰ The behavior was first observed in a single individual in 1980 and has subsequently spread to many hundreds of whales in the region. Detailed recording and analysis of the diffusion of this behavior has established that lobtail feeding is a learned trait, which individuals acquire through copying, and which has spread among close associates in a social network.¹¹ Young whales acquire this highly productive feeding method from older individuals, with the skill passed from one generation to the next as a cultural tradition.

Moving away from the wilds to an Emory University laboratory, researchers in 2014 were astonished by some laboratory mice that mysteriously exhibited a fear experimenters had trained into their grandparents.¹² That is not supposed to happen! For over a century, generations of students have been taught that the inheritance of acquired characteristics is a biological impossibility.¹³ A mouse should not be born with knowledge that its ancestors learned during their lifetimes as this clearly violates Weismann's barrier. The "barrier," proposed in 1892 by German evolutionary biologist August Weismann, captures the hypothesis that the cell lineages that produce sperm and eggs are separated from the rest of the body early in development, and hence that whatever happens to the body cannot be inherited. Famously, Weismann severed the tails of mice, observed no reduction in tail length among their offspring, and declared Lamarckian inheritance refuted.¹⁴

Of course, Weismann was unaware of epigenetic inheritance. The DNA in the nuclei of cells is not naked but clothed in a variety of chemically attached molecules that affect the level of expression of nearby genes.¹⁵ "Methylation" refers to the addition of a methyl chemical group to one of the DNA nucleotide bases.¹⁶ When methyl groups are added to DNA they can suppress the activity of a gene, while their removal can lead to that gene's expression. The Emory University researchers showed that when mice were conditioned to be frightened of a particular smell, their offspring, and their offspring's offspring, retained this fear. That is because the odor entrainment had modified the *Olfir151* gene, which encodes the olfactory receptor specific for this odor, by removing a methyl group from it. Remarkably, this *demethylation* of the *Olfir151* gene was also seen in the sperm of these mice, and indeed their offspring's sperm.¹⁷ The inheritance of such methylation patterns across generations is now well established in plants and some animals.¹⁸ What is still unclear is how events in the mouse's central nervous system triggered demethylation

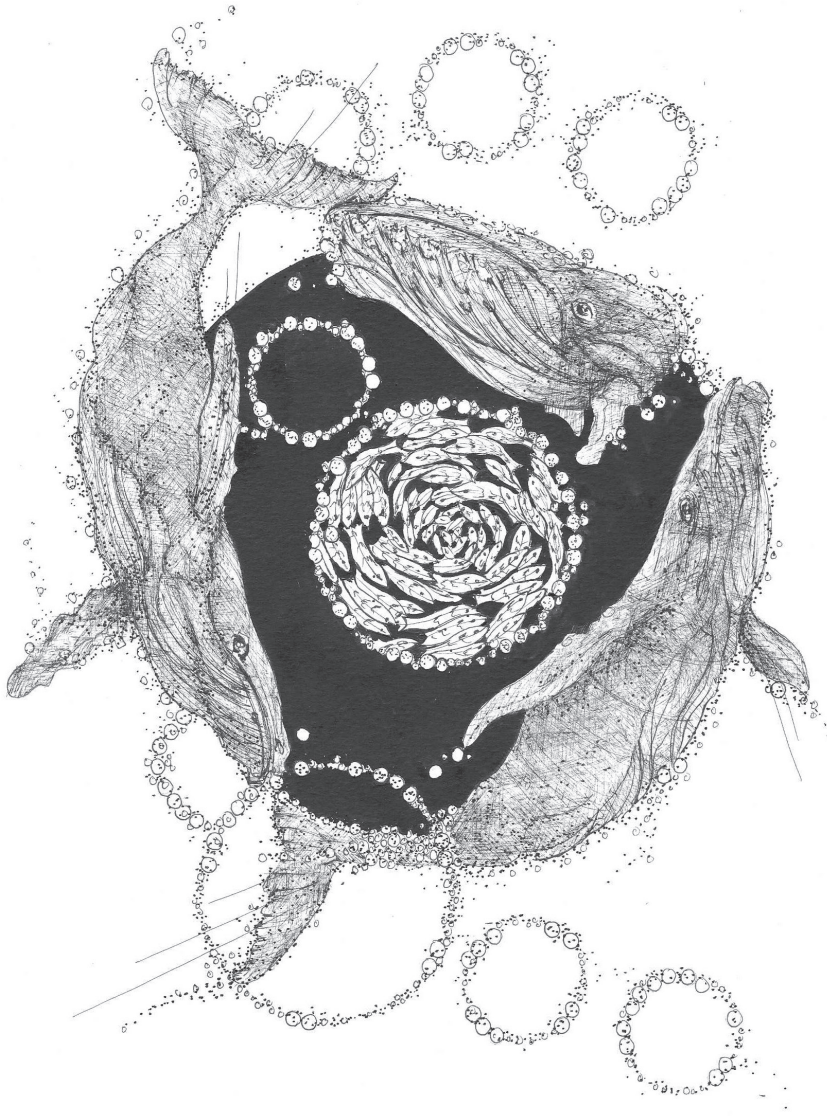


FIGURE 2. Humpback whales possess highly distinctive traditions that are learned and culturally inherited. For instance, whales in some populations in the northeast Pacific collaborate in small groups to catch prey by coordinating their bubble net feeding, while humpbacks in the Gulf of Maine prey on sand lance through a learned innovation known as “lobtail feeding.” Each population has its own song, which evolves over time too rapidly to be explained by genetic evolution. These behaviors are passed across the generations by cultural transmission, independently of inherited genetic variation.

in their sperm, but one empirically demonstrated pathway involves the transfer of noncoding RNAs to the sex cells,¹⁹ which has also been found to underlie the epigenetic inheritance of learned information in nematode worms.²⁰

These three examples, in different ways, defy the classical view of heredity as mediated solely by gene transmission, and challenge our understanding of how evolution works. Generations of desert woodrats are reliant on other species' genes to exploit a novel foraging niche, and their trait of feeding on a toxic food is stable only because of resources reliably extracted from their ecological environment. The ability to exploit detoxifying enzymes confers a clear fitness advantage, and in the case of the woodrats there is evidence that natural selection has acted on this heritable phenotypic variation.²¹ The example is so dramatic that it may come as a surprise that these rodents are broadly representative of many organisms that are equally dependent on their live-in microorganisms to carry out essential functions.²² Corals rely on microalgae for energy production, legumes require bacteria for nitrogen fixation, and cows couldn't eat grass without the microbial community inside their rumen.²³ Symbiotic microorganisms can be passed from one generation to the next along diverse nongenetic pathways, including inside eggs, seeds, and embryos and through suckling, eating others' feces, or consuming regurgitated foods.²⁴ Even when symbionts are acquired from the external environment rather than from parents, they can still be surprisingly reliably transmitted, as the woodrat example illustrates.²⁵ Transgenerational microbial transmission is now recognized as a common, perhaps universal, component of animal inheritance.²⁶

The humpback whales are passing foraging information that appears to enhance their biological fitness across the generations through cultural transmission, independently of inherited genetic variation. Biologists have long been aware of cultural inheritance, but have tended to regard it as a special case, germane only to humans. This belief is no longer tenable. In the last fifty years, vast evidence for "culture" has emerged through scientific investigations of a broad array of animals, both in their natural environments and in the experimental laboratory. Numerous species transmit learned knowledge through imitation and other forms of social learning, including dietary information, feeding techniques, predator recognition and avoidance methods, songs and calls, learned migratory pathways, and mate and breeding-site choices.²⁷ There are now—quite literally—thousands of scientific reports of learned behaviors spreading through natural animal populations by these means.²⁸ Familiar examples include common chimpanzees fishing for termites with sticks, birds

drinking from milk bottles, and birds and whales transmitting songs.²⁹ Animal culture does more than contribute to inheritance, however. It allows groups of animals to adjust their behavior to match their environment. In the case of the humpback whales, the “adaptations” needed to hunt locally abundant prey did not arise through genetic mutation and natural selection, but via behavioral innovations spread through cultural transmission. Recent analysis suggests that lobtail feeding is a local refinement of the more widespread bubble net feeding, which is similar to lobtail feeding but doesn’t involve the initial tail slap that stuns the fish. Intriguingly, other humpback populations in the northeast Pacific have refined bubble net feeding in a different way, creating a new cooperative strategy where groups of whales coordinate their bubble net foraging. In this North Pacific culture, individual whales take on distinctive roles, with some whales releasing bubbles, others making feeding calls, and all or most members of the group feeding (figure 2).³⁰ In some species—humans included—culture has become the principal means by which the animal adapts to its environment, giving rise to a new form of adaptability.³¹ What is more, the spread of cultural knowledge is driving genetic evolution.³² For instance, killer whale populations have socially learned specializations for particular prey (e.g., fish, dolphins, pinnipeds), and these specializations favored population-specific morphologies and digestive physiologies, known as *ecotypes*, among which reproductively isolated groups emerged.³³ Here, culturally learned dietary traditions have initiated and modified the natural selection of genes associated with morphologies and physiologies that match the whales’ learned habits, imposing a direction on genetic evolution.³⁴

And the frightened mice represent a “ripping up of the rule books” concerning how biology works and what can and cannot be inherited, as the field of epigenetics reveals hitherto inconceivable mechanisms and phenomena that defy time-honored understanding. Epigenetics is a rapidly developing field of science, and a bewildering variety of mechanisms for the regulation of gene expression have been identified.³⁵ While historically it was widely accepted that Weismann’s barrier prevented environmentally induced changes from altering the germline (i.e., eggs and sperm), in recent years the immutability of Weismann’s barrier has been undermined by experimental research demonstrating that epigenetic changes can be inherited in a wide variety of organisms.³⁶ There is clear evidence that epigenetic changes can strongly affect the fitness of individuals, can be subject to natural selection, and can facilitate genetic adaptation. Experiments in yeast, for instance, show that the natural selection of epigenetic changes can help populations to acquire a genetic

resistance to toxins, and when experimentally deprived of this capability, populations often go extinct.³⁷

Neither inherited microbiomes nor animal cultures nor epigenetic inheritance is rare in nature, as this book will make clear. A veritable cornucopia of resources other than genes are now known to be passed down the generations, including components of both egg and sperm, hormones, symbionts, epigenetic changes, antibodies, ecological resources, and learned knowledge.³⁸ For a century, “soft inheritance”—the view that heredity can be changed by lifetime experiences—was regarded as disreputable.³⁹ The doyen of evolutionary biology, Ernst Mayr, asserted that “the greatest contribution of the young science of genetics [was] to show that soft inheritance does not exist.”⁴⁰ Today, soft inheritance seems to be everywhere.

Nor is it solely biologists’ understanding of heredity that is being challenged. In recent years, science has revealed that there is so much exchange of genetic material across lineages that Darwin’s “tree of life” now resembles a tangled network.⁴¹ What we thought were individual organisms have turned out to be communities, which is just one of several reasons why the developing organism can no longer be parsed tidily into separate “genotype” and “phenotype” components, with the former exerting exclusive control over the latter.⁴² The familiar suggestion that genes contain “instructions” is being reassessed, as the information to build bodies is distributed across numerous inherited resources and reconstructed during development.⁴³ Novel insights and findings like the above are pouring out of biological laboratories at a rate that leaves many researchers reeling. The challenge is to make sense of it all!

The founders of the modern evolutionary synthesis laid great emphasis on the distinction between the lifetime of an individual organism from conception to death (its “development”) and the biological history of the species (its “evolution”).⁴⁴ Rightly or wrongly, the view became prevalent that the processes and mechanisms underlying evolution could safely be studied without knowledge of the processes and mechanisms responsible for development.⁴⁵ For almost a century developmental biology and evolutionary biology were mostly separate fields.⁴⁶ Repeated attempts were made to bring these disciplines back together, but never with more than partial success.⁴⁷

Now, after decades of waxing and waning, enthusiasm for developmental insights is waxing again in the evolutionary community. Invigorated by advances in experimental and theoretical methods, science is shedding new light on the developmental origins of phenotypic variation, evolutionary innovation, adaptation, speciation, and macroevolutionary patterns. This is not without

controversy. The evidence that the mechanisms of cellular, molecular, and developmental biology might facilitate the generation, selection, and inheritance of adaptive phenotypic variation has been accompanied by a lively debate.⁴⁸ The authors of this book have, in various ways, been active participants in this discussion, an experience that has taught us much, and honed our perspective. We are convinced that the differences of opinion extend beyond the issue of how best to incorporate new biological knowledge, and also relate to how the history of the field is understood, as well as to philosophical issues concerning the scientific process.⁴⁹ Part of the controversy also arises from assumptions, often unstated, about how developmental processes generate phenotypic variation. That the pioneers of our perspective—notably Conrad Waddington, Richard Lewontin, and Mary Jane West-Eberhard—each emphasized in their writings that developmental processes are constructive, open-ended, and contingent, and above all not “genetically programmed,” we suggest is no coincidence. Accordingly, we devote considerable attention to explaining key aspects of developmental biology, while trying to avoid too much technical detail.

Much of the debate over the role that developmental processes play in evolution relates to how researchers regard the subprocesses that underly natural selection. Harvard evolutionary biologist Richard Lewontin identified three such subprocesses: (1) there must be variation in characteristics among individuals in a population (*phenotypic variation*), (2) some variants must leave more descendants than others (*differential fitness*), and (3) offspring must resemble their parents more than they resemble unrelated individuals (*heredity*).⁵⁰ However, the historically dominant view that natural selection is the sole cause of adaptive evolution is tied to the additional, less-apparent assumption that the three subprocesses are effectively autonomous: they feed into one another, but do not modify one another’s operation.⁵¹

Cases like the desert woodrats or the killer whales raise the possibility that developmental mechanisms do more than simply generate variation: they also modify the processes that contribute to differential fitness (e.g., when behavior learned from nonrelatives affects survival) and to heredity (e.g., when symbiotic bacteria are passed on to descendants via the ecological environment). In such instances, the three subprocesses underlying evolution by natural selection become intertwined, and understanding natural selection becomes more challenging. Current controversies concerning extragenetic inheritance (a.k.a. *nongenetic inheritance*),⁵² whether developmental mechanisms constrain or facilitate evolution (i.e., *developmental bias*), whether developmental responses to environmental change can direct genetic change (i.e., *plasticity*-

led evolution), and how the activities and outputs of organisms modify selection (i.e., *niche construction*), relate to interactions between Lewontin's subprocesses. An exciting implication of the aforementioned new data is that the evolutionary process itself evolves, as the characteristics of evolving populations and their modes of inheritance influence how natural selection operates. To make sense of it all, evolutionary researchers may need to reconsider both the structure of evolutionary theory and the nature of evolutionary explanations. These themes are the focus of this book.

In 1973, the influential evolutionary biologist Theodosius Dobzhansky boldly asserted that “nothing in biology makes sense except in the light of evolution.”⁵³ Nearly fifty years later, leading evolutionary biologists worry that “nothing in biology makes sense anymore” and accept the “monumental challenge of making sense of a rapidly growing menagerie of discoveries that violate deeply ingrained ideas.”⁵⁴ Here, by contrast, we argue that there is a natural order, a richness, and even an elegance to adaptive evolution implied by the “new biology”—but its comprehension requires thinking more broadly about evolution. Two fields of biology that historically became separated need to be brought back together. Dobzhansky's famous assertion can be rescued if paired with the reciprocal dictum: *nothing in evolution makes sense except in the light of development*.⁵⁵

INDEX

Page numbers in *italics* refer to figures and tables

- Abzhanov, Arkhat, on expression of *Bmp4* gene, 193–94
 acetylcholine, 215
 adaptation(s): adaptive behavior and, 283n34; camels and desert plants, 119–20; definition of, 284n39; desert extremes, 122; diversification and, 28–29; evolutionary biology, 20; survival of dark and pale mice, 40
 adaptive evolution, 13; developmental bias and, 92–96; development constraining, 234; direction, rate and equilibrium states of, 229; natural selection as sole cause, 42; transformational explanation, 239; variational explanation, 239
 adaptive evolutionary change, 28–29
 adaptive improvisation, 70
 adaptive landscapes: developmental mechanisms and, 136, 137; dynamic, 134–38
 adaptive radiation, diversification and, 111–13
 agriculture, human evolution and, 217–18
 Aiello, Leslie, on expensive-tissue hypothesis, 321n58
 Alberch, Pere, on digit development, 275n93
 animal(s): evolvability of, 314–15n80; language of, 221; learning, 68, 69; learning American Sign Language, 327n163; plasticity and, 116–18
 animal culture, 125, 300n198; definition, 292n30; extragenetic inheritance, 148, 161–65; horizontal transmission, 164; social learning, 163, 164; transmission of information, 162–64
Anolis lizards: adaptive radiation of, 112–13; morphology, 280n98; natural experiments of, 21
 Antarctic conditions, emperor penguins and, 127–28
 ants: adaptive developmental pathways of, 179–80; exploratory mechanisms, 68, 69; as large-headed “supersoldiers”, 179–80; wing-forming GRNs, 179
 apes, bipedality of, 207
 aphids, *Buchnera aphidocola* and, 181
 Arabian oryx, 121
Arabidopsis thaliana: DNA methylation in, 155; epigenetic inheritance, 243; epigenetic variation in, 154, 201, 202; morphological traits, 92; selection, 154, 201
 archosaurs, 28
 Arnold, Stevan, on selection gradient, 138
 associative learning, 323n76
Astyanax mexicanus, 100–106, 102.
 See also blind Mexican cave fish (*Astyanax mexicanus*)
 Badyaev, Alexander, on hormonal regulation, 111
 Baldwin, James Mark, on plasticity and evolution, 107
 Bateson, William: genetics, 304n2; on polydactyly, 307n82
 behavioral ecology, subfield, 27
 behavioral innovations, social learning, 116–17
 Belyaev, Dmitry, breeding wild foxes, 83, 85
 bet hedging, 313n60; heritable form of, 154–55, 168
 bias, 16, 94; development principle, 79.
 See also developmental bias

- bichir fish: plasticity and innovation in, 180, 207; social learning, 198; traits of, 180–81
- Bicyclus* butterflies, eyespot size and color, 191
- bighorn sheep, 164, 301n208
- Bilandžija, Helena, on raising *Astyanax mexicanus*, 101
- biological evolution, role of development in, 38–39
- biological fitness, 7
- bipedalism, 318n8, and human evolution, 207–11
- birds' beaks, morphological diversity of, 95
- blastula, 52
- blind Mexican cave fish (*Astyanax mexicanus*), 232; developmental mechanisms, 125–26; domestication syndrome and, 142; facial bone fragmentation, 105; investigations of, 242; lens transplantation, 104–5; natural selection, 103–4; phenotypic plasticity, 106; plasticity and, 196–97; plasticity-led evolution, 100–106, 102
- blood vessels, 69
- Bmp4*, expression, 75; amount and timing of expression of, 193–94
- body mass index (BMI), 152
- Bonduriansky, Russell, on nongenetic inheritance, 33
- bone fragmentation, cave fish populations, 105
- bonobos, 207
- Braendle, Christian, on nematode worms, 92
- brain(s): development, 69; human cognition and, 211–15; size of, 323n82
- Brakefield, Paul, model species *Bicyclus anynana*, 94–95
- British Eugenics Society, 260n83
- Broca's area, 213
- Brown University, 32
- Bruce, Heather, on leg exites forming wings, 175–76
- Buchnera aphidicola* (bacterium), aphids and, 181
- bumblebees, microbiome of, 161
- Bumpus, Hermon, on size of house sparrow, 32
- butterflies: evolutionary history of, 22; evolvability of, 203; habitats and food availability, 141
- butterfly (*Bicyclus anynana*), 66; developmental control of eyespots, 94–95; eyespot color, 310n8
- Caenorhabditis elegans*: developmental bias illustration, 92; experimental evolution, 293n46
- Caenorhabditis briggsae*, developmental bias illustration, 92
- Cain, Arthur, on selection in natural populations, 32
- Cambrian explosion, body plans in, 185
- camels: adaptation, 283n7; desert plants and, 119–20; evolution of, 138–39; hump size, 287n122
- canalization, 107
- caterpillar (*Adelpha serpa*), adaptation, 20
- cause of selection, term, 138
- cell(s): role of mechanical forces, 63–65; self-assembly, 60, 61–63
- central dogma, Crick's, 31
- character identity networks, 305n8
- Charlesworth, Brian, on evolutionary genetics, 241, 245
- childbirth, humans, 208–9
- Childs, Barton, on neural developmental plasticity, 324–25n102
- chimpanzees: bipedality of, 207; brains of, 211; pelvis shape of, 209
- Chimpsky, Nim (chimpanzee), 327n164
- Chomsky, Noam, on language, 328n166
- circuits, 57
- cis-regulatory elements, 53
- cleavage, division, 52
- climate change, 21
- CNRS-University of Nice, nematode worms, 92
- Cockayne syndrome, 75
- cognition: human brain and, 211–15; human evolution, 216
- cognitive gadgets, human brains and, 222
- cognitive salience, evolutionary criteria, 17, 19
- Cold War, 31
- Columbia University, 29
- competition, sexual selection and, 141
- concerted evolution, cognition, 213

- consequence laws, evolutionary theory, 124–25
- constraints, 16, 94; conception of, 98; evolution of necks, 87–88; phenotypic variation, 16; structured phenotypic variation as, 87
- constructive, development principle, 75, 77
- cooking: digestion system and, 211; invention of, 219
- coprophagous transmission, termites, 115
- corals, energy production, 7
- covariation, 17; traits, 17
- Crick, Francis, 31; central dogma, 31; sequence hypothesis of, 257n44; sequence of nucleotide bases, 78
- cross-talk, developmental pathways, 73
- cultural evolution, 5–8, 40–41, 161–65, 202, 211–12, 219–20, 225
- cultural inheritance, 5–8, 40–41, 148, 149
- cultural variation, 300n195; animal cultural differences, 161–65
- culture: animals and, 5–8, 40–41; 161–65, 202, 211–12; cultural adaptation term, 41; cultural drift, 334n63; human evolvability, 202, 219–20, 225; human evolution, 225; cultural information, 162
- Curvularia*, heat stress and, 159
- Cybernetics, 260n84
- “cyclopia”, 104
- cytoskeleton, 69
- Darwin, Charles: on challenge of human evolution, 206; on domesticated species, 209; evolutionary biology, 21; evolutionary theory, 173; finches, 231; on gender roles, 217; on gradualism, 33; on human language, 220, 222; on social learning of bees, 162; theory of evolution, 238–39; theory of inheritance, 83; traits and domestication, 270–71n4
- Darwinism, 226; beauty and simplicity of, 228
- Darwin’s finches, 193–94; evolvability, 204
- Darwin’s “tree of life”, 9
- Dawkins, Richard, concept of genetic determinism, 259n74
- Day, Troy, on nongenetic inheritance, 33
- Deacon, Terrence, on brain development, 213
- debates, rescuing strategies for selection, 43–46
- defense priming, 153
- degree of integration, evolutionary criteria, 17, 18–19
- demethylation, *Olf* 151 gene, 5
- deoxyribonucleic acid. *See* DNA (deoxyribonucleic acid)
- Descent of Man, The* (Darwin), 220, 255n2, 318n2
- desert environment: adaptations, 119–22; humans in, 121–22, organisms and, 141
- desert rhubarb, 120, 121; physiology of, 141
- desert snails, 121, 283n24
- desert woodrats, 3–5, 240. *See also* woodrats; woodrats, desert
- detection: environmental cues, 155; evolutionary adaptation, 166
- development: assessment of evolutionary role of, 240; conception to death, 9; constraining evolution, 232; debate on conceptions of, 38–39; evolution and, 11, 35–37, 46; genetic program, 232–33; term, 51. *See also* developmental processes; principles of development
- developmental bias, 10, 43, 44, 125, 190; adaptive evolution and, 92–96; behavior generating, 117–18; concept of, 89; developmental process, 235; diversification and, 310n20; domestication syndrome and, 84; embracing, 96–99; evolution and adaptation, 16; evolutionary biology textbooks on, 331n21; genetic channeling and, 17; genus *Heteropsis*, 96; human evolution, 223; natural selection and, 47, 89, 99; nematode worms (*Caenorhabditis elegans* and *C. briggsae*), 92; niche construction as form of, 198–201; phenotypic variation vs. variability, 89–92; recognizing as cause of evolution, 99; selection and, 87–89; term, 14
- developmental biology: evolutionary and, 11, 231
- developmental constraint, topic of, 245
- developmental constraints, 13–14, 87
- developmental genetics, 265n41
- developmental mechanisms: adaptive landscapes, 136, 137; domestication syndrome and, 134; environments and, 108–9
- developmental plasticity, innovation through, 178–81

- developmental processes, 10; control of, 71; Darwinian, 69; directionality on natural selection, 240–41; epigenetics of, 59–67; evolvability, 205; exploratory, 67–71; exploratory mechanisms, 69; genetics of, 52–59; Lewontin's criteria for selection, 235; mathematical theory, 312n46.
See also epigenetics of development; genetics of development
- Dias, Brian, on offspring and grand-offspring of experimental mice, 34
- differential fitness, 10, 128; dung beetles, 236, 237; evolution by natural selection, 38, 39, 233–34; variants, 122
- Diffugia*: cell structure of, 148; Weissmann on, 33
- digestive system, human evolution and, 210–11, 224
- digit patterning, vertebrate, 183–85
- discontinuous variation, challenge of, 174–75
- diversification: adaptation and biological diversity, 241; adaptive radiation and, 111–13; developmental bias and, 310n20; niche construction and, 200–201
- DNA (deoxyribonucleic acid): adaptation of fossil dog feces, 158; coding sequences of, 92–93; methylation of nucleotide base, 156; nucleotide bases, 293n53
- DNA methylation, 5, 279n80; epigenetic inheritance, 151, 152, 156
- DNA to RNA to proteins, information flow, 31
- Dobzhansky, Theodosius: on biology and evolution, 11; on *Drosophila* morphology, 36; evolutionary biologist, 173; natural selection and adaptation, 31; on rates of evolution, 310n6, 331–32n24
- dogs, gut microbiome, 158, 159
- dolphins, social learning, 250n28
- domesticated animals, as Darwin's inspiration, 83
- domestication syndrome, 319n30; artificial selection during, 83, 84; blind Mexican cave fish and, 142; developmental bias, 88–89; developmental experiments, 229–30; developmental mechanisms and, 134; gene regulatory network (GRN) and, 133; mammals, 83–86; natural and artificial selection, 86; neural crest cell, 275–76n101; neural crest cells and, 85; neural crest model for, 272n16
- dopamine, 215
- Down syndrome, 271n7
- Drosophila*: features of wing, 192, 232, 242; genetics of, 35–36; mutation in, 263n22; wing patterns, 274n63
- Drosophila melanogaster* (fruit fly), 29
- dung beetles: brood-ball processing, 235, 236; development, 240; head horns of, 176; horn development, 288n128; insulin/insulin-like signaling pathway (IIS) of, 178–79; intertwining of variation, fitness and inheritance, 236, 237; investigations of, 242; larval niche construction, 281n112; niche construction and selection, 141; self-inhibition of developmental modules, 177; “sneaker” morphs of, 289n139; traits, 238
- dung beetles (*Onthophagus*): horn formation, 305n27; niche construction, 114–15, 126–27, 140, 199, 238
- Dutch Hunger Winter, 151, 152, 295n73, 295n75
- earthworms: ecological legacy, 42; niche construction, 42–43
- ecological developmental biology, label, 244
- ecological inheritance, 42–43, 148, 149, 149; dung beetles, 237
- ecology, 46; evolution and, 33; importance in evolution, 127
- ecomorphs, *Anolis* lizards, 280n98
- ecosystem engineering, 287n105
- ecotypes: killer whales, 40; learned specializations, 163; patterns of natural selection, 40
- ectoderm, outer layer, 52
- egg smearing, 157
- embryo, self-assembly of, 61–62
- Emory University, 34; mice and inherited fear, 5
- emperor penguins, 127–28
- ENCODE project, 258–59n72, 270n36
- Endler, John, selection in natural populations, 32
- endoderm, inner layer, 52–53

- endogenous retroviruses, DNA sequences, 182
- endurance running, definition, 208, 318n13
- endurers, 127; camels as archetypical, 120
- enhancers: cell-type-specific, 54; genes, 53
- environment(s): camels and desert, 119–20; life's inductive gamble, 128–31; niche construction and external, 113–15; outside world, 66–67; termites, 120–21
- environmental stress, inherited microbiota, 238
- environment detection, 162
- epigenetic, term, 59
- epigenetic inheritance, 44, 125; bet hedging, 154–55, 168; definition, 292n30; DNA methylation, 151, 152, 156; extragenetic inheritance, 150–57; genetic mutations, 156, 157; on heritable silencing of a gene, 155–56; histone modification, 151, 156; noncoding RNAs, 151; topic of, 245
- epigenetic silencing, genetic assimilation of mutations, 201
- epigenetics, 46; developing field of, 8; development principle, 73–75; inheritance of fear in mice, 41–42; term, 150, 250n15, 263n5, 265n41, 269n12
- epigenetics of development, 59–67; built by symbionts, 67; inescapable outside world, 66–67; physical and chemical forces, 60–61; role of mechanical forces, 63–65; structure from external cues, 61–63
- epigenetic variation, 297n122; adaptive parental, 295n73; genetic and, 295–96n88
- epigenic inheritance, 148, 149
- eugenics, 257n42; term, 260n83
- evo-devo: blind Mexican cave fish, 101; evolutionary novelty, 175; subfield, 27
- evo-devo research: developmental mechanisms, 255n14; eyespots of butterflies' wings, 94–95
- evo-devo studies, 17, 18; evolvability, 204; turtle embryos, 24–25
- evo-devo study, evolutionary novelty, 187–88
- evolution: adaptive, 13, 92–96; biological history of species, 9; biology and, 11; cave fish populations, 105; constraints of, 272n26; definition of, 333n62; description of, 96–97; developmental bias as cause of, 99; developmental perspective of, 251–52n48; development and, 35–37; development constraining, 232; Dobzhansky on, 11; of evolvability, 203–5; historical roots of explanation, 28–34; models of, 284n52; natural selection and, 262n47; of plasticity, 118; process of, 240–41; requirements for, by natural selection, 38–39; research agenda for twenty-first century, 241–44; role of plasticity in, 126; understanding of, 228–30. *See also* cultural evolution; plasticity-led evolution
- evolutionary adaptation, embracing developmental bias, 96–97
- evolutionary approach: cognitive salience, 17, 19; criteria for alternative explanations, 17–19; degree of integration, 17, 18–19; factual accuracy, 17, 19; nonsensitivity, 17, 18; precision, 17–18
- evolutionary biology, 169, 256n32, 318n3; adaptive change as feature of, 47; development relevant to, 79; developmental biology and, 231; developmental bias and, 97; developmental processes, 245; evolution of, 230–41; fields of, 27; goals of, 20, 21; historical roots of, 28–34; pluralism in, 22, 24–25, 27–28; predictive science, 15–16; progress in, 46–47; source laws for, 124–28
- evolutionary biology textbooks, 331n21
- evolutionary causation: emerging view of, 245; niche construction and, 43; phenotype covariation, 97–98; rescuing strategies for selection, 43–46; understanding, 142, 240
- evolutionary community, developmental insights of, 9–10
- evolutionary developmental biology, 17–18, 244; label, 244. *See also* evo-devo
- evolutionary ecology, blind Mexican cave fish, 101
- evolutionary game theory, 257–58n49
- evolutionary geneticists, 254n32
- evolutionary genetics, 241
- evolutionary history, reconstructing, 20–21
- evolutionary novelty, insect wing 174–75
- evolutionary processes, changing gene frequencies, 230
- evolutionary synthesis, vision of, 228–30

- evolutionary theory, development of, 244–47
- evolution of evolutionary process, research agenda, 243–44
- evolvability, 189–205; animals, 314–15n80; concept of, 309n1; definition of, 282n146; evolution of, 203–5; extragenetic inheritance and, 201–3; genetic, 314n71; genetic bases of reciprocal causation, 192–95; human, 206–26; introduction of genetic variation, 190–92; new forms of, 247; niche construction as form of developmental bias, 198–201; properties conferring, 189–90; role of plasticity, 196–98. *See also* human evolution
- exceptionalism, human, 206, 225
- exites: outgrowths, 175; wing formation from, 175–76
- exploratory processes (*a.k.a.* exploratory mechanisms): evolutionary implications of, 68, 69, 77, 116, 130, 198, 207, 246; key aspect of development, 67–71
- extended evolutionary synthesis, x , 333n61; label, 244
- extragenetic inheritance, 10, 43, 44–45, 145, 190, 233; animal culture, 148, 161–65; breadth of, 145, 148–65; components of, 290n2; developmental process, 235; epigenetic inheritance, 148, 150–57; evolutionary adaptation, 166; evolutionary biology textbooks on, 331n21; evolvability and, 201–3; inherited microbiome, 148, 157–61; instability of, 316n112; long-term adaptation, 166; parental effects, 148–50; plasticity and, 261n33; redirecting genetic evolution, 167; term, 290n6. *See also* inheritance
- eyespot, developmental control of, 94–95
- facial bone fragmentation, cave fish populations, 105
- Factors of Evolution* (Schmalhausen), 260n84
- factual accuracy: evaluating explanations, 45; evolutionary criteria, 17, 19
- Farm-Fox Experiment, 271n8
- Ferguson-Smith, Anne, DNA studies, 294n63
- fish (*Phycodurus eques*), adaptation, 20
- Fisher, Ronald: on eugenics, 257n42, 260n83; fundamental theorem, 135–37; integrating Mendelian genetics and mathematical models, 30, 256n32
- fitness differences: causes of, 139; evolutionary explanations and, 142–43; natural selection and, 45; research agenda, 242–43
- “flexible stem” hypothesis, West-Eberhard’s, 111–12
- Fogarty, Laurel, on quantitative-genetic model of evolutionary consequences, 239
- food procurement, human evolution and, 217–18
- foraging: bighorn sheep, 164, 301n208; green wave surfing, 301nn208–9
- Ford, Edmund, on selection in natural populations, 32
- fossils, turtle shell, 28
- fox genus *Vulpes*; skull morphology of, 86
- frogs, polyphenism, 109–110
- fruit flies: inheritance, 29, 30; microbiome of, 159–60; wing morphology, 92. *See also Drosophila*
- G** matrix, 17, 18, 253n28, 254n34, 316n112, 332n38; variance-covariance, 191, 197
- $g_{\max}$, greatest genetic variation, 17, 90, 253n28, 254n34, 254n44
- Gale, Emily, on digit development, 275n93
- Galton, Francis, eugenics movement, 260n83
- gastrulation, 52
- gender roles, Darwin on, 217
- gene(s), 78; “beads on a string”, “string on the beads”, 53; combination of, 53–54; containing instructions, 9; enhancers, 53; expression, 52; heredity and, 233; plasticity and, 107–11; regulation, 51–52
- gene-culture coevolution, mathematical modelling, 220
- gene regulatory networks (GRNs), 36, 55; complexity of, 58–59; computational models of, 264–65n36; construction of, 57; control of development, 71; domestication syndrome, 133; evolution of, 193; exoskeletal development, 72; genes and, 305n15; organization of, 57; production of phenotypes, 58; topology of, 57–58;

- underlying cave fish traits, 102; wing-forming, 179
- genetic accommodation: natural selection, 112; response, 280n96
- Genetical Theory of Natural Selection, The (Fisher), 260n83
- genetic architecture: label, 312n36; term, 269n18
- genetic assimilation, 106, 107, 156, 167; *Astyanax mexicanus*, 103; response, 280n96
- genetic channeling: developmental bias and, 17; hypothesis, 17
- genetic covariation, 142
- genetic determinism, concept of, 259n74
- genetic evolution, cultural knowledge, 8
- genetic information, predicting the future, 165–68
- genetic inheritance, 148, 149; dung beetles, 236, 237
- genetic mutations, 156, 157
- genetic program, 65; development, 232–33; idea of, 259n74
- genetics, 46; development, heredity, and evolution, 35–37; *Drosophila* morphology, 35–36; term, 304n2. *See also* quantitative genetics
- genetics of development, 52–59; gene regulatory networks (GRNs), 57–59; neural crest cells, 55–57
- genetic variation: introduction of, 190–92; selection and, 231–32
- genome: holobiont, 161; programmed development, 77
- genotype, 9; definition, 251n42; definition of, 333n62; phenotype and, 29–30; plasticity as properties of, 245
- genotype-phenotype map (G-P map), 91, 273n51; label, 312n36; term, 269n18, 312n36
- genotype space, 23; biological explanation, 76
- germline transmission, inheritance pathway, 148, 149
- González-Forero, Mauricio, on evolutionary pathways across landscapes, 135
- Gould, Stephen Jay: dialectical materialism, 260n84; evolutionary biology, 187; leading evolutionist, 36; on mammalian evolution, 12
- G-P map. *See* genotype-phenotype map (G-P map)
- gray matter, outer cortical layer, 61
- green wave surfing, foraging, 301nn208–9
- Gulf of Maine, 4; humpbacks in, 6
- gyrification, folding in tissues, 60–61
- Haldane, J.B.S., integrating Mendelian genetics and mathematical models, 30
- “hand in glove” idiom, 120
- Hardy-Weinberg law, 256n32
- Harvard Medical School, 294n63
- hemoglobin sickle cell (*HbS*) allele, 217–18
- herbivores, teeth of, 13
- herbivory, evolution of, 115, 142
- heredity, 10, 128, 144; developmentalist view of inheritance, 168–69; evolution by natural selection, 38, 39, 233–34; forecast, 169, 304n254; foundational concept of, 169; genes and, 233; idealizations, 34; Johannsen defining, 29; term, 291n10
- heritable variation, constraining evolution, 17
- heterochrony, 25
- Heteropsis* genus, control of eyespot, 96; eyespot color, 195
- heterotopy, 25
- histone modifications, 293n54
- holobiont, development of, 67; evolution of, 146, 161
- Holocaust, 31
- Homo* genus, evolution of running in, 208
- Homo* species, brain size and, 320n44
- Homo erectus*, 216
- Homo ergaster*, 216
- Homo habilis*, tool use by, 216
- homology: concept, 188; definition in biology, 174
- hopeful monsters, 205, 318n135
- hornworm moth (*Manduca quinqueaculata*), polyphenism, 110
- host-microbiome relationships, niche construction, 140
- Houle, David, on fruit fly wings, 192
- Houri-Zeevi, Leah, on epigenetic inheritance in nematodes, 153
- human dentition, evolutionary changes, 210–11

- human evolution, 206–7; agriculture and food procurement, 217–18; bipedality and gracile morphology, 207–11; brain development, 214–15; childbirth, 208–9; culture and, 225; developmental bias and, 223–24; gender roles of tool use, 217; human brains and cognition, 211–15; innovations, 207; language, 220–23; mechanisms of, 223–26; tool use, 216–20
- human exceptionalism, 206, 225
- human genome, sequences from viruses, 182
- humans: brain circuitry during evolution of, 322–23n73; brain evolution, 212, 320n45, 320–21n50, 322n64, 322n69; brain shape and face shape, 321–22n61; desert environments and, 121–22; microbiome inheritance, 298n128; observational learning, 325n116; as planning animals, 324–25n102
- human sciences, 46
- humpback whales: foraging information, 7; lobtail feeding, 4–5, 6, 8, 235; traditions of, 6
- Huxley, Julian: British Eugenics Society, 260n83; on eugenics, 257n42
- Huxley, Thomas, as champion of Darwin's ideas, 173
- Hydra*, coevolution of microbes, 160
- idealizations, 22; bias, 28; scientific process and, 23; shaping research agendas, 34
- immunity, exploratory mechanism, 68, 69
- indirect genetic effects (IGEs), 281n112
- inductive gamble, life's, 128–31
- information, cultural transmission, 162–64
- inheritance: cultural, 4–8, 40–41, 148, 149, 161–65; developmentalist view of, 168–69; ecological, 148, 149, 149; epigenetic, 5, 8–9, 145, 148, 149; epigenetics, 145; forms of, beyond genes, 144–45; genetic, 148, 149; germline transmission, 148, 149; parental effects, 148–50; predicting the future, 165–68; research agenda, 243; soft forms of, 145, 148, 149; soma-to-environment-to-soma transmission, 148, 149; soma-to-germline transmission, 148, 149; soma-to-soma transmission, 148, 149. *See also* extragenetic inheritance
- inherited microbiome: definition, 292n30; extragenetic inheritance, 148, 157–61
- inhibitory cascade model: adaptive diversification of teeth, 14; phalangeal variation, 14–15; tooth development, 13, 210; trait covariation and evolvability, 18
- innovation: animal body plans, 178; bichir fish, 180; co-option of developmental circuitry, 175–77; developmental plasticity, 178–81; evolutionary, 177; novelty and, 174–75; regulatory networks, 312n45; symbionts, 181–82; term, 174; threshold effects, 182–85
- insulin/insulin-like signaling pathway (IIS), dung beetles, 178–79
- intelligence, collective, 162
- interchangeability, development principle, 77–79
- internal selection, 311n30
- Jablonka, Eva, on extra-genetic inheritance, 145
- Jacob, Francois, idea of genetic program, 259n74
- jawbones, gaping behavior of, 64–65
- Jeffery, William: on cave and surface fish, 277n25; on raising *Astyanax mexicanus*, 101
- Jennings, Herbert, on structural inheritance, 34
- Jernvall, Jukka, on tooth morphology, 12
- Jesmer, Brett, on translocated bighorn sheep, 301n208
- Johannsen, Wilhelm: defining heredity, 29; distinction of genotype and phenotype, 251n42, 304n254
- Just, Ernest Everett, 286n80
- Kaplan, Hillard, on brains and cognition, 212
- Kavanagh, Kathryn, on tooth morphology, 12
- kernels, 185
- Kessler, Kerry, on offspring and grand-offspring of experimental mice, 34
- Kettlewell, Bernard, on selection in natural populations, 32
- killer whales, 10, 240; evolutionary explanation, 43–44; foraging habits, 40, 41; natural selection and, 40–41; social learning, 250n28
- Kirschner, Marc, on evolution, 252n55

- Lamarckian, 259n81; adaptation, 167;
doctrines, 36; evolution account, 239;
inheritance, 5, 304n254, 333n49
- Lamarckism, 30
- Lamb, Marion, on heredity and inheritance,
145
- Lande, Russell, on selection gradient, 138
- language: American Sign Language,
327n163; brain circuitry of, 221; children
and use of, 329n185; Chomsky on,
328n166; cultural evolution of, 329n182;
evolution of, 220–23; primate vocaliza-
tions, 220–21; teaching and tools
for thought, 328n170; vocal learning,
327n162
- learned behavior, 68, 69, 116–18
- learned knowledge, 7–8
- learning: adaptation, 301–2n215; observa-
tional, in humans, 325n116; vocal,
327n162
- lens transplantation, blind cave fish, 104–5
- Levins, Richard, dialectical materialism,
260n84
- Lewontin, Richard: on “auto mechanics”,
124; beetle niche construction, 140–41;
developmental processes, 10, 235; dialectical
materialism, 260n84; essays on
niche construction and adaptation,
246; on evolution by natural selection,
38, 241; leading evolutionist, 36; on
organisms and environment, 246; on
population genetics, 123–24; on se-
lection of organisms, 134; subprocesses,
11; on variational and transformational
explanations, 238
- Lichtman, Jeffery, on nervous system,
325n102
- life cycle, multicellular organisms, 52
- lobtail feeding, 4–5; humpback whales,
4–5, 6, 8
- Louis, Ard, on RNA secondary structures,
93–94
- Lysenko, Trofim, on acquired inheritance,
257n45
- Lysenkoism, 31, 259n82
- M** matrix (mutation matrix), 191, 192, 197,
273n44, 332n38
- macroevolutionary patterns, understand-
ing, 185–87
- mammalian domestication, 85–86. *See also*
domestication syndrome
- mammalian neck, evolution of, 87–88
- mammalian teeth, development of, 12–13
- mapping, genotype-to-phenotype (G-P)
translation, 74
- mating preferences, 209, 319n25
- Mayr, Ernst: evolutionary biologist, 173;
as first “population thinker”, 31; idea of
genetic program, 259n74; on natural
selection, 39–40; natural selection and
adaptation, 31; on proximate-ultimate
distinction, 230, 257n47; on soft inheri-
tance, 9; variation in color patterns,
32–33
- mechanical forces, role of, on cells, 63–65
- mechanotransduction, process, 63
- meiosis, 151
- melanocortin-1 receptor (*Mcl1r*) gene,
mice, 39–40
- Mendelian genetics, 30, 145; cause of
heredity, 29
- Mendelian inheritance, 256n32
- Mendel’s Laws, 304n2
- Mendel’s work, rediscovery of, 29
- mesoderm, middle layer, 52
- messenger RNAs (mRNAs), 62
- methylation, 5
- mice: adaptation in, 39–40; epigenetic
inheritance of fear in, 41–42; tooth size
variation, 98
- microbiome, 3, 9, 238; animal culture and,
167; description of, 157; inherited, 148,
157–61, 298n128; Mojave woodrats, 158
- missing heritability, 152
- Mitf* gene, 57
- Mivart, George, religious apologist, 173
- Moczek, Armin, on dung beetle niche
construction, 139–40
- modularity, development principle, 72–73
- Mojave Desert woodrats, 4; adaptations
of, 3; detoxification adaptations of, 7,
250n21; digesting creosote, 133; Great
Basin Desert, 249n6; microbiota of, 3,
158. *See also* woodrats, desert
- molar teeth, morphology of, 12–13
- Morgan, Thomas Hunt: *Drosophila* labora-
tory of, 35–36; reconceptualization of
heredity, 29, 253n26
- morphology changes, humans, 209–10

- morphospace, concept of, 13
 motifs, 57
 Muller, Hermann: on eugenics, 257n42;
 eugenics movement, 260n83
 Müller, Max, on language, 327n158
 mutations: developmental modules,
 311n25; environment and beneficial, 108.
 See also **M** matrix
- natural selection, 10; adaptation by, 68;
 camel adaptations, 119–20; cave fish
 populations, 126; conception of evolu-
 tion by, 39; criteria for evolution by,
 233–34; developmental bias and, 47,
 97, 99; development bias and, 87–89;
 ecotypes and patterns of, 40; evolution
 and, 262n47; favoring small eyes, 103–4;
 fitness differences and traits, 142–43;
 framing of evolution by, 46; genetic
 inheritance and, 223; genetic variation
 and, 231–32; human evolution, 224;
 language evolution, 222–23; niche con-
 struction and, 42; origin of life and,
 229; population genetics, 123–24;
 requirements for evolution by, 38–39;
 on “source laws” and “consequence laws”,
 124–25; study of, 33. *See also* selection
- Natural Selection in the Wild (Endler), 32
 nature, nurture and, 227
 Neanderthals, 321n60
 nematode worms (*Caenorhabditis elegans*
 and *C. briggsae*), developmental bias
 illustration, 92
 neoteny, phenomenon, 209
 nervous system, development of, 68
 neural crest cell genes, 271n11; mutations,
 271n15
 neural crest cells, domestication syndrome,
 85
 neural tube, 53
 neuronal connections, 69
 neuroscience, origins of language, 221
 niche-constructing activities, 42
 niche construction, 11, 42–43, 113–15, 125,
 190; adaptive plasticity and, 130; co-
 variation and selection, 315n94; desert
 extremes, 122; developmental plasticity
 and, 135; diversification and, 200–201;
 dung beetles, 114–15, 126–27, 140, 238;
 earthworms, 42–43; ecological inheri-
 tance and, 287n105; evolutionary biol-
 ogy textbooks on, 331n21; as form of
 developmental bias, 198–201; herbivory
 and, 115; host-microbiome relationships,
 140; human evolution, 224–25; human
 populations and, 218; intact and experi-
 mentally reduced, 285n67; plasticity
 and, 128; plasticity-led evolution and
 human, 218–19; quantitative-genetic
 model of evolutionary consequences,
 239; technological development and,
 219–20
 niche construction theory, 259n79
 Nijhout, Frederik, artificial selection experi-
 ment, 110
 nongenetic inheritance, 10
 nonsensitivity, evolutionary criteria, 17, 18
 novelty: definition, 305n8; innovation and,
 174–75; study of evolutionary, 187–88;
 term, 174
 nurture, nature and, 227
- obstetric dilemma, arising from pedality, 214
Olfr 151 gene, demethylation of, 5
Onthophagus (dung beetles), niche con-
 struction, 114–15
 organicism, 35
 organicist movement, 35
 organisms: environment properties, 66–67;
 life’s inductive gamble, 128–31
 origin of life, natural selection and, 229
Origin of Species, The (Darwin), 31, 206,
 284n47
 Osmanovic, Dino, on Darwinian selection,
 161
 Oyama, Susan, on developmentalist
 thinking, 79
- paleontology, 46; subfield, 27
*Pangenesi*s, inheritance through, 83
Paramecium, cell structure of, 148
 parental effects: definition of, 149; extrage-
 netic inheritance, 148–50; adaptive, 153;
 anticipatory, 153
 Parkinson’s disease, 215
 Parsons, Kevin, on skull morphology, 86
 Patel, Nipam, on leg exites forming wings,
 175–76
 Patti, Mary-Elizabeth, DNA studies,
 294n63

- Pax6* gene, 54; eye field, 104
 pelvic floor hypothesis, 318n20
 persistence hunting, running and, 208
 phalanges: finger and toe bones, 14,
 253n24; phalangeal variation, 14–15;
 sizes of toe bones, 15
 phenocopies, 106; environmental effect, 104
 phenotype, 9; definition, 251n42; defini-
 tion of, 333n62; developmental regula-
 tion, 75; gene regulatory networks
 (GRN) and, 58; genotype and, 29–30;
 inheritance of medical phenotypes,
 330n203
 phenotype space, 23; biological explana-
 tion, 76
 phenotypic plasticity, 100, 190; desert
 extremes, 122; development, 178;
 developmental process, 235; speciation
 and adaptive radiation, 111–13
 phenotypic traits, causes of differences in,
 29
 phenotypic variability, evolution of,
 192–93
 phenotypic variation, 9, 10; constraints, 16;
 development, 79; dung beetles, 236, 237;
 evolution by natural selection, 38–39,
 233–34; population, 122; research
 agenda, 241–42; supply and demand, 97;
 variability vs., 89–92
 photosynthesis, 227
 phylogenetic constraints, 14
 Physical Basis of Heredity, The (Morgan),
 256n30
PIM3, methylation of, 153
Pitx1 gene, 54–55
 plant populations, analyses, 279–80n93
 plasticity, 43, 44, 100, 125; bias and, 45;
 bichir fish, 180; blind Mexican cave fish,
 196–97; evolutionary biology textbooks
 on, 331n21; evolution and adaptive, 108,
 112, 129–30; evolution of, 118; extrage-
 netic inheritance and, 261n33; forms
 of, 70; genes and, 107–11; human brain,
 215; human evolution, 224; learning and
 behavior, 116–18; niche construction
 and, 128, 130; properties of genotypes,
 245; role in evolution, 113, 126; role
 in evolvability, 196–98; selection for,
 314n71. *See also* developmental plastic-
 ity; phenotypic plasticity
 plasticity-first evolution, 109. *See also*
 plasticity-led evolution
 plasticity-led evolution, 10–11; animal
 body plans, 178; blind Mexican cave
 fish, 100–106, 102; diversification and
 adaptive radiation, 111–13; evolution of
 plasticity, 118; human niche construction
 and, 218–19; learning and behavior,
 116–18; niche construction, 113–15;
 plasticity leads, genes follow, 107–11;
 topic of, 245
 plastron, 25, 26
 pleiotropy, term, 271n7
 polydactyly: digit loss and, 307n77; digit
 patterning, 183; humans and vertebrates,
 182–83; phenotype and, 307n82;
 reaction rate and, 307n76
Polygonum: epigenetic inheritance, 243;
 inbred genotypes of, 153; inherited
 adaptations to light and shade, 166
 polyphenism, 66, 107; dung beetles, 179;
 frogs and toads, 109–10
 population genetics: Lewontin describing,
 123–24; types of, 286n74
 predictive adaptive responses, 153
 primates: culture, 211–12; vocalizations of,
 220–21
 principles of development: bias, 79; con-
 structive, 75, 77; epigenetic, 73–75;
 interchangeability, 77–79; modular,
 72–73; regulatory networks, 76
ptch1 gene, 64–65
 Purves, Dale, on nervous system, 325n102
 quantitative genetics, 276n102; evolution-
 ary, 90–91; evolvability, 204; genetic
 covariation pattern, 90; phenotypic
 evolution as, 89–90
 quantitative genetic theory, 277–78n50,
 288n129
 Rampelli, Simone, on fossil dog feces in
 Italy, 158
 Raup, David, on snail shell shapes, 93
 reactive genome, 78
 reciprocal causation, 16; genetic bases of,
 192–95
 redirection, evolutionary adaptation, 166
 red-winged blackbirds, learned behavior of,
 116

- regeneration, studies of, 268n116
- regulatory network, 76, 273n51, 305n8;
 - G-P map, 194; higher-level interactions, 75; term, 312n36
- rescaling, 45; evolutionary explanation, 43; killer whales, 44; mammalian teeth, 44
- research agenda: evolution, for twenty-first century, 241–44; evolution of evolutionary process, 243–44; fitness differences, 242–43; inheritance, 243; phenotypic variation, 241–42
- RNA (ribonucleic acid): genotype-phenotype relationship for, 93, 94; Louis on structures of, 93–94; noncoding RNAs, 151; plasticity and evolvability in, 282n146, 314n71; secondary structure, 95, 234–35; structure of, 91, 232
- robustness, developmental mechanism, 317n128
- Rohner, Patrick, on dung beetle niche construction, 139–40
- Roughgarden, Joan, on symbiont transfer, 161
- San Roman, Magdalena, on evolution investigation in bacteria, 186
- Scaphiopus* species (tadpoles), polyphenism, 109–10
- Schluter, Dolph, on evolution in three-spined stickleback, 16–17
- Schmalhausen, Ivan, embryology and evolutionary biology, 260n84
- Schmid, Marc, selection experiments of *Arabidopsis*, 154
- Schwab, Daniel, on dung beetle niche construction, 139–40
- scientific process, idealization and, 23
- sea slug, 227–28
- selection: distinguishing between selection of and selection for, 131–34; dynamic adaptive landscapes, 134–38; evolutionary adaptation, 166; gradients, 138–39; life's inductive gamble, 128–31; phenotypic variation, 155; practical implications, 138–43; sexual, 138, 141; understanding, 122–24; variation and, 195, 200. *See also* natural selection
- selection machine: association between ball size and color, 133; balls in, 132; Sober on toy as, 131
- self-assembly, structure from external cues, 61–63
- Selfish Gene, The* (Dawkins), 259n74
- self-stimulatory mechanisms, 65
- sex determination, 313n54
- sexual dimorphisms, dung beetles, 179
- sexual selection: competition and, 141; Tanaka modelling, 138
- Simpson, George: evolutionary biologist, 173; natural selection and adaptation, 31
- Smith, John Maynard: on understanding genetics, 33; on Weismann's concept of separation of germline and soma, 251n45
- Sober, Elliot: on “source laws” and “consequence laws”, 124; terminology, 284n49; toy as “selection machine”, 131, 286–87n97
- Sober, Elliott, on variational and transformational explanations, 238
- social learning, 7–8; foraging strategies, 250n28; primates, 213
- social network, whales, 5
- soft heredity, 30, 144–69
- soft inheritance, 9, 145, 256n30, 258n70
- soma-to-environment-to-soma transmission, inheritance pathway, 148, 149
- soma-to-germline transmission, inheritance pathway, 148, 149
- soma-to-soma transmission, inheritance pathway, 148, 149
- sonic hedgehog gene (*Shh*): domain size, 277nn35–36; eye-forming field, 104, 197; point mutation in cis-regulatory element, 182–83
- source laws, evolutionary theory, 124
- spadefoot toads (genus *Spea*): plasticity-led evolution, 109–10; polyphenism of, 109–10
- speech, brain circuitry of language and, 221
- squid *Euprymna scolopes*, 67
- Stajic, Dragan, on heritable silencing of a gene, 155–56
- Stebbins, Ledyard, on mutation and evolution, 310n6, 331n24
- stickleback fishes, learning of, 116–17
- Sultan, Sonia: inbred genotypes of plant *Polygonum*, 153; on *Polygonum* in drought conditions, 154
- Suzuki, Yuichiro, artificial selection experiment, 110

- symbionts: inheritance, 157–61; innovation through, 181–82; role in development, 67; viral, in evolutionary innovation, 182
- symbioses, host animals and plant-digesting microorganisms, 115
- symbiotic microorganisms, nongenetic pathways, 7
- tadpoles (genus *Scaphiopus*), plasticity-led evolution, 109–10
- Tanaka, Mark: modeling adaptive evolution on landscapes, 135, 137; modeling sexual selection, 138
- technology, human evolution, 216–20
- teeth: development of mammalian, 12–13; inhibitory cascade model of tooth development, 13; mastodon molars, 12; inhibitory cascade model of tooth morphology, 14
- Tel Aviv University, 153
- termites, adaptive complementarity, 120–21
- Testudines, turtle order, 24
- Theoretical Biology Club, 35, 36, 259n79
- Theory of the Gene*, *The* (Morgan), 29
- thermoregulation, 208
- threshold effects, innovation through, 182–85
- toads, polyphenism, 109–10
- tool use, 213; human evolution, 216–20
- tooth. *See* teeth
- trait(s): covariation, 142; genetic variation and, 190–91; origination of novel, 173; troglomorphic, of cave-dwelling, 101
- transcription factors: DNA sequences, 54; enhancer regions of genes, 53; phenotypes and, 55
- transgenerational immune priming, 295n80
- transgenerational inheritance, 333–34n63; cultural adaptation and, 41
- transplantation of fish lens, blind cave fish, 104–5
- trans-regulatory elements, 53
- “tree of life”, Darwin’s, 9
- Tribolium* hornless species, 176
- Turing, Alan: framework of patterns, 63; models, 307n69, 307n72; reaction-diffusion models, 183–84; Turing process, 317n128
- turtle shell(s): carapace, 24, 26, 27–28; development of, 26, 27; evolution of, 24–25
- universal design principle, 253n26
- University of Cambridge, 294n63
- University of Glasgow, 86
- University of Maryland, 101
- University of New Mexico, 212
- University of Oxford, Ard Louis’s lab at, 93
- University of Wyoming, 301n208
- University of Zurich, 154, 186
- Uppsala Multigeneration Study, 294n63
- Usher’s syndrome, 75
- variability, 91; phenotypic variation vs., 89–92
- variation, 128; selection and, 195, 200; temperature and humidity of environment, 129
- Vegf* gene, 70
- vertebrates: digit patterning, 183–85; polydactyly in, 182–83
- vertebrate skeleton, development and growth of, 63–64
- Vibrio fischeri*, 67
- viral symbionts, evolutionary innovation, 182
- Waddington, Conrad: conceptions of epigenetics, genetic assimilation and exploitive system, 246; developmental processes, 10; on epigenetics, 35; evolutionary biology, 187; on genetics of *Drosophila* morphology, 35–36; on plasticity and evolution, 107; on population and evolution, 144; term “epigenetic”, 59; on unknown future of organisms, 169
- Wade, Michael, on quantitative-genetic model of evolutionary consequences, 239
- Wagner, Andreas, on evolutionary investigation in bacteria, 186
- Wagner, Günter, character identity networks, 305n8
- wasp *Asobara*, 77
- water fleas (*Daphnia magna*), epigenetic inheritance, 294n69
- Watson, James, on DNA sequence, 75
- weak regulatory linkage, mix-and-match process, 73
- Weismann, August: on barrier in development, 5, 8, 34, 145; concept of separation of germline and soma, 33, 251n45; experiment of cutting tails of mice, 33–34

- Wesleyan University, 153
- West-Eberhard, Mary Jane: on developmental plasticity, 246; developmental processes, 10; evolutionary biology, 187; flexible stem hypothesis, 111–12; on genes in evolution, 107; leading evolutionist, 36; on proximate-ultimate distinction, 230, 254n31; on statistical interaction, 90
- Western bluebirds, nest-site competitors, 141
- Wheeler, Peter, on expensive-tissue hypothesis, 321n58
- Whitehead, Alfred North, on organicism, 260n84
- Wilkins, Adam, on neural crest cells, 83, 85
- Wnt* and *Bmp* (genes), 268n1; balance of, 56; expression pattern, 73; roles in patterning, 183; signaling pathways, 72
- woodrats, desert, 10; creosote bushes, 3, 294n8; creosote resin, 3, 249n2; Great Basin Desert, 249n6; gut microbiome, 159; microbiome of, 160; microbiota of, 3; Mojave Desert, 3, 4; natural selection for, 7; technical names for, 249n1. *See also* desert woodrats; Mojave desert woodrats
- World War II, exposure to famine, 151
- Wrangham, Richard, on human digestive system, 210
- Wright, Sewall: integrating Mendelian genetics and mathematical models, 30; on polydactyly in guinea pigs, 307–308n83
- yellow pigment cells, 63
- Zattara, Eduardo, on novel compound eye, 177
- zygote: genome, 53; inheriting DNA, 78; life cycle, 52