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PART I

Introduction
Why Consider Development?

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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]

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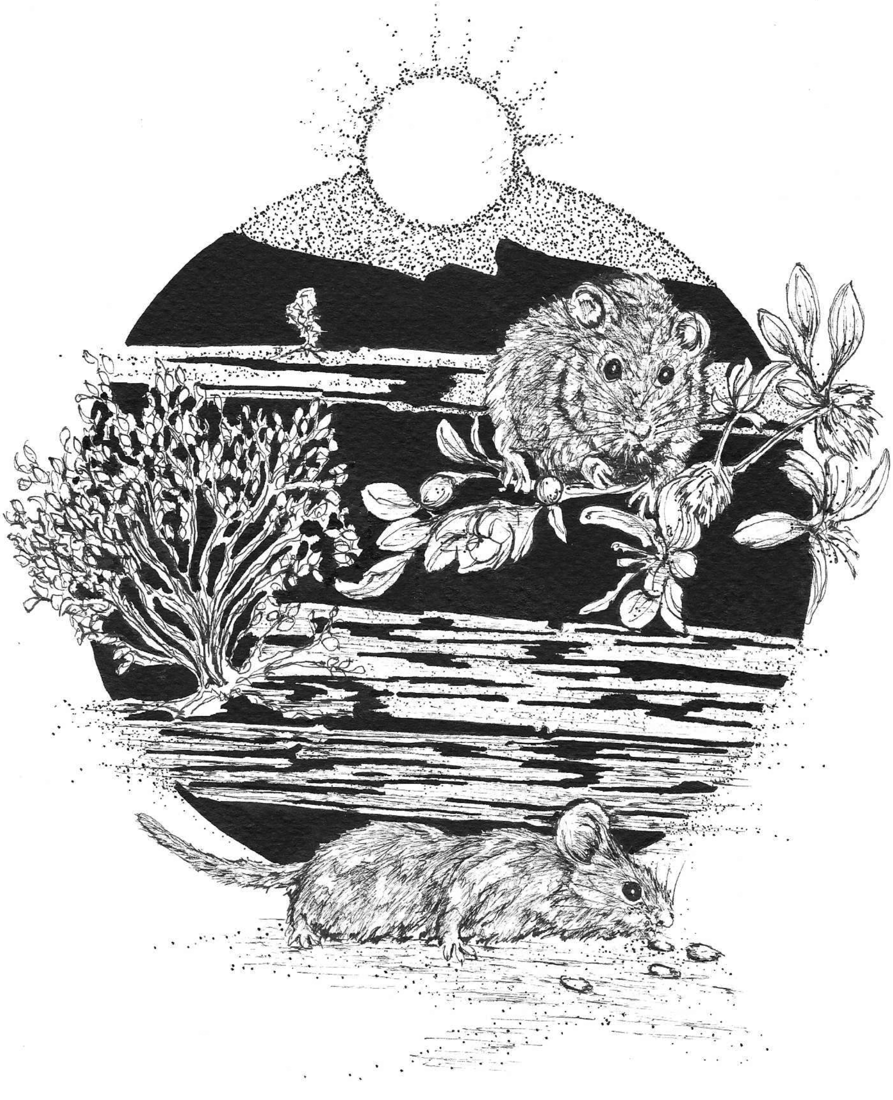

FIGURE 1. Mojave Desert woodrats feed on a toxic diet, thanks to bacteria that they reliably inherit by consuming soil and feces in their environment.

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

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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 corralled 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 *Olfr151* gene, which encodes the olfactory receptor specific for this odor, by removing a methyl group from it. Remarkably, this *demethylation* of the *Olfr151* 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

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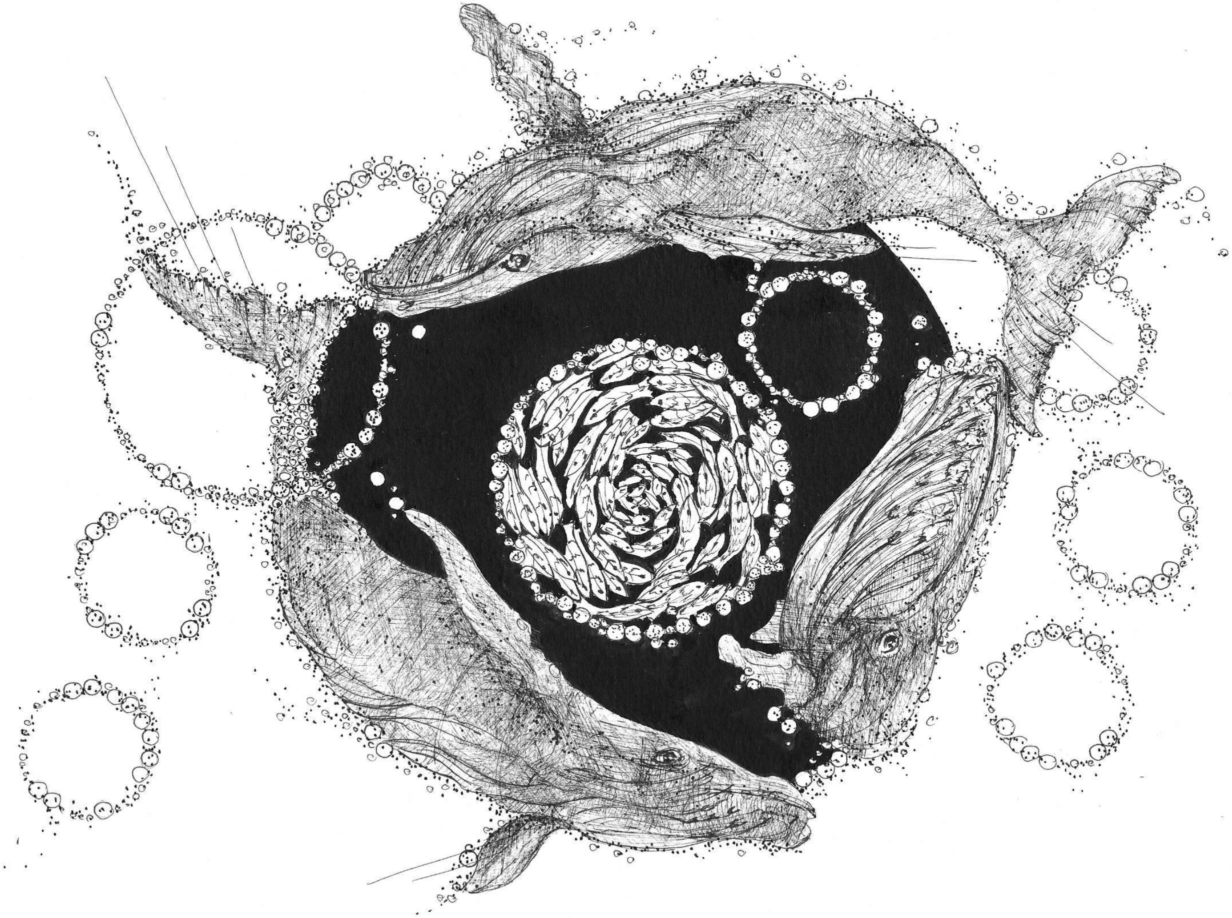

FIGURE 2. Humpback whales possess highly distinctive traditions that are learned and culturally inherited. For instance, whales in some populations in the northeast Pacific collaborate in small groups to catch prey by coordinating their bubble net feeding, while humpbacks in the Gulf of Maine prey on 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.

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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

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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

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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

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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-*

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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]

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