1 A Darwinian Introduction

In this chapter I outline Darwin's theory of evolution, indicating which parts survive in modern biology and which have been discarded.[1]

1.1 Common Ancestry

Figure 1.1 is the only illustration that Darwin included in his 1859 book *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. He used it to represent some of the main elements of his theory. The figure depicts a phylogenetic tree in which objects at the top of the page exist now, and as you go down the page you're going back in time, tracing items at the top to their recent and more remote ancestors. You can think of the objects at the top as current species, though Darwin's picture also applies to single organisms alive today. There are fifteen objects at the top of the figure, but they descend from only three of the objects (A, F, and I) at the bottom. If you trace those three back in time, they will eventually coalesce into a single common ancestor. Modern biology agrees with Darwin, in that the standard view now is:

> **Universal Common Ancestry:** All the organisms now on earth descended from a single common ancestor.

This thesis does not mean that life evolved from non-living materials only once. Universal common ancestry is compatible with numerous start-ups. There also is no requirement that only one of those start-ups managed to have descendants that are alive today. To see why, compare Darwin's Figure 1.1

[1] Darwin's theorizing evolved in his lifetime, on which see Ruse (1979) and Ospovat (1981). In this book, I use the term "Darwin's theory" to refer to what appeared in the first edition of the *Origin* and was further articulated in subsequent editions of that book and in his subsequent writings.

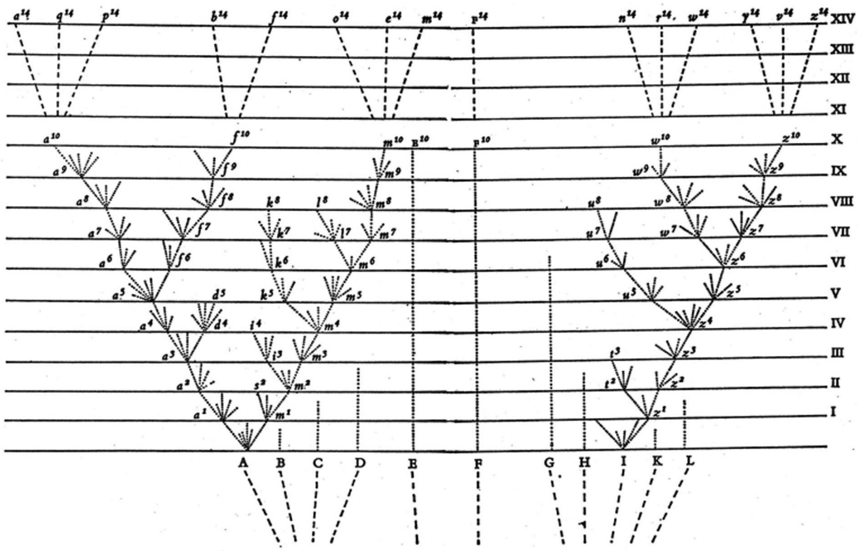

Figure 1.1 The Tree of Life in Darwin's *Origin of Species*.

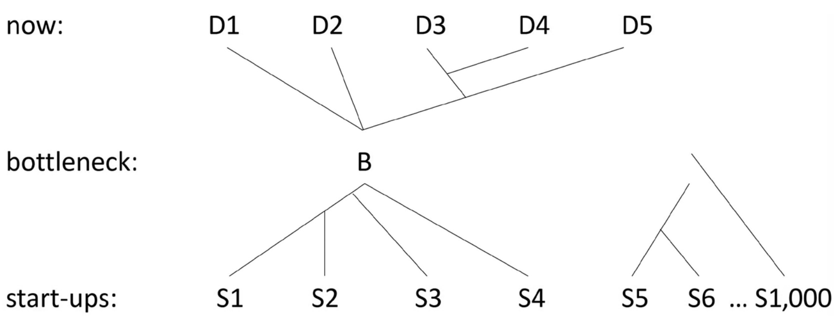

Figure 1.2 A phylogenetic bottleneck in which there is universal common ancestry.

with the genealogy shown in Figure 1.2, which includes 1,000 start-ups, four of which founded lineages that then merged; the result is a universal common ancestor of all living things on the planet today. The genealogy in Figure 1.1 is a *tree* in the technical sense of that term: Branches split but never join as your eye moves from past to present. The genealogy in Figure 1.2 is not a tree; biologists use the term "reticulation" to describe the joining.

Darwin was a resolute tree thinker, but the question of whether life's genealogy is tree-like is now debated. Some biologists regard the Tree of Life as an outmoded concept, given that pairs of plant species have often

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hybridized to produce new species, and given also that organisms often have genes that didn't come from their parents but were inserted by the horizontal transfer of genes from a contemporaneous organism in a different species. However, other biologists think the Tree of Life idea is true often enough, especially for eukaryotes (organisms whose cells have nuclei), for it to remain a valuable idea. See Doolittle (2000) for discussion.

1.2 Species

The title Darwin gave to his 1859 book may lead you to think that the species category occupies a very special place in his theory. If so, the following remark from the *Origin* (Darwin 1859, p. 52) may surprise you: "I look at the term species as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety." When a parent in Darwin's diagram has several descendant lineages, the descendants will count as conspecific varieties if they diverge only modestly, but if they become more different from each other, they will count as distinct species. There is no bright line that separates the one situation from the other. Darwin denies that there are "walls" that prevent old species from evolving into new ones. This no-walls thesis follows immediately from common ancestry.

Most present-day evolutionary biologists disagree with Darwin's relaxed view of the difference between species and varieties. One of the most influential species concepts in modern evolutionary biology is Ernst Mayr's (1970) *biological species concept*. It holds (roughly) that two populations belong to the same species precisely when individuals in the two populations interbreed and produce viable fertile offspring. For Mayr, subspecific varieties are different in kind from species, properly so called. I'll discuss species in Chapter 7.

1.3 Evolution

Whereas the vertical dimension in Darwin's Figure 1.1 represents time, the horizontal dimension represents phenotypic similarity.[2] Objects

[2] *Phenotype* is a garbage-can category denoting any feature of an organism that is not genetic in character; it includes all traits of morphology, physiology, and behavior.

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A and B in the figure are more similar to each other than A and C are, and A and L are more dissimilar than any other pair of early objects. Biologists who now draw phylogenetic trees usually don't use the horizontal dimension in this way; in modern biology, trees represent genealogical relatedness alone.

In Figure 1.1, descendants almost always differ phenotypically from their ancestors. If evolution just means that lineages change their characteristics, then there is evolution aplenty in Darwin's diagram. But is the equation of evolution with character change correct? Suppose that nutrition improves in a starving population with the result that descendants are bigger and healthier than their ancestors. That would not be enough for modern biologists to conclude that the population has evolved. The definition often used now is that evolution is change in the genetic composition of populations.[3] Phenotypic change without genetic change isn't evolution. Unfortunately, the genetic definition is too narrow. The genetic system is itself a product of evolution. This entails that the existence of genes is not a prerequisite for evolution to occur.

What did Darwin mean when he talked about lineages evolving? Darwin (1859, p. 12) says that he restricts his attention to traits that are *inherited*. This raises the question of what inheritance means. In ordinary English, you can say that people sometimes "inherit" money from their parents, but that's not how Darwin used the term. Darwin had in mind the traits that are transmitted from parents to offspring *in the biological process of reproduction*. Gregor Mendel was a contemporary of Darwin's, but Darwin knew nothing about Mendelian genes. Modern biology reveals that the transmission of material from parents to offspring in reproduction involves more than just genes. There is non-genetic material in

This usage is compatible with the fact that many phenotypes are causally influenced by genes. The distinction between *what X is* and *what causes X* is important here. An organism's phenotype can include things that are outside its skin; the fact that a spider spins a particular type of web is a phenotypic trait the spider has. The elaboration of this idea has been the project of *niche construction theory*, which is part of what is called *the extended evolutionary synthesis* (Laland et al. 2015).

[3] This definition is broader than the definition of evolution as change in gene frequencies. The problem with the gene frequency definition is that the frequencies of single genes can remain constant while the frequencies of gene combinations change, and biologists will readily count the latter as instances of evolution. Sober (1993) illustrates this possibility by an example involving assortative mating.

both eggs and sperm. The new field of *epigenetics* studies that additional dimension of transmission.[4]

You may think that fossils provide conclusive evidence that evolution has occurred. After all, many fossils differ markedly from the organisms we now see around us. In fact, the observed features of fossils, by themselves, don't entail that evolution has occurred. However, universal common ancestry plus the fact that current organisms differ in their inherited traits suffices for evolution to have occurred. Fossils are icing on the cake.[5]

1.4 Divergence and Opportunism

Returning to the horizontal dimension of Figure 1.1, you'll notice that there is more diversity now than there was at the time of A through L. Darwin drew broken lines from A through L back into a more remote past, and he slanted those lines to indicate that there was still less diversity at that earlier time. Modern biology rejects the idea that diversity steadily increases. Mass extinctions have diminished diversity – several times, and drastically. True, when life first began there was minimal diversity, and now there is lots more. But in between, diversity has waxed and waned.

Darwin has diversity steadily increasing in Figure 1.1 because he endorsed the following principle:

> **The Principle of Divergence**: The immediate descendants of a common ancestor tend to do better at surviving and reproducing if they have extreme phenotypes, and worse if they have middling phenotypes. (Darwin 1859, p. 117)

Darwin's (1859, p. 76) idea was that individuals with extreme phenotypes usually have fewer competitors than individuals with middling phenotypes, and so the extremists do better in the struggle for existence. In other words, extremists tend to be *fitter* than middle-of-the-road organisms, and so the process of *natural selection* will favor the evolution of more extreme trait values over trait values that are middling. For Darwin, that's why diversity increases. To check whether Darwin's Figure 1.1 conforms to his Principle

[4] This expanded conception of inheritance is part of what is now called the extended modern synthesis (Laland et al. 2015).

[5] In Section 7.10, I'll explain why a fossil can provide stronger evidence than an extant organism about the traits of their most recent common ancestor.

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of Divergence, you can trace the objects that exist now back in time, counting how often they derive from middling ancestors and how often from extremists.

Modern biology has abandoned this part of Darwin's theory. The Principle of Divergence is often untrue. Birth weight in humans is a classic counterexample; newborn babies of middling weight on average do better than babies who are smaller or larger. However, the problem with Darwin's principle goes deeper. It isn't just that there are exceptions to the Principle of Divergence. There is no such thing as the one and only phenotype that "tends" to evolve when there is natural selection. For example, organisms that are more complex often outcompete organisms that are simpler, but the reverse pattern is common as well. Darwin (1859, p. 148) cites an example of the latter when he notes that parasites are often simpler than their free-living ancestors. George Gaylord Simpson (1967, p. 160) expressed this idea by saying that natural selection is *opportunistic*. Which traits are fitter than which others almost always depends on accidental features of the environment.

The opportunism of evolution by natural selection contrasts starkly with the idea that evolution is *pre-programmed*. Jean-Baptiste Lamarck (1809) proposed an evolutionary theory of this type. According to Lamarck, life emerges repeatedly from non-living materials and then increases in complexity by moving through a fixed sequence of stages.[6] Lamarck's theory denies that *current* human beings and *current* worms have a common ancestor, although it asserts that *current* human beings had worm-like *ancestors*. We human beings belong to a very old lineage, since that lineage had to evolve through a long sequence of simpler stages. Current worms, being simpler than humans, trace back to a more recent start-up. Lamarck's theory denies universal common ancestry.

1.5 Selection – Natural, Artificial, Sexual, and Bi-leveled

Although the Principle of Divergence is not part of modern biology, one of Darwin's ideas about natural selection is now mainstream:

[6] This is the primary evolutionary process in Lamarck's theory, but he adds a secondary process in which organisms diversify so as to adapt to their environments (e.g., when giraffes evolve longer necks so they can reach leaves at the top of trees). This is where Lamarck's idea of the inheritance of acquired characteristics comes into play, an idea I'll discuss in Section 1.6.

Natural Selection is a pervasive and important cause of evolution.

Natural selection is Darwin's explanation for why only three of the eleven lettered objects in Figure 1.1 managed to have descendants that are alive today. Individuals that are better able to survive and reproduce outcompete individuals that are less able to do so. Natural selection causes some lineages to go extinct and others to persist. In the *Origin*, Darwin (1859, p. 6) says that "natural selection has been the main but not the exclusive cause" of evolution. Darwin's mention of "main" entails that natural selection is more important than other causes of evolution. Notice that the thesis I formulated above about natural selection is more modest. I'll explain in Chapter 8 why I've steered clear of the word "main."

Darwin distinguishes natural selection from artificial selection. Artificial selection is what farmers do when they decide which plants and animals in one generation will be permitted to reproduce. Artificial selection involves conscious choosing; natural selection, in contrast, can be mindless. If the weather gets colder, there may be selection for thicker fur in a species of bears, with the consequence that bears with thicker fur survive and reproduce more successfully than bears with thinner fur. The weather is not a conscious agent.[7]

Darwin also contrasts natural selection with sexual selection. He says that sexual selection occurs when males compete with each other for access to females, and also when females choose the males with whom they'll mate. A consequence of the former is that male elephant seals are far larger than females. A consequence of the latter is that peacocks have gaudy tails, whereas peahens do not. It is odd that Darwin thought of male combat and female choice as falling outside the category of natural selection. It also is noteworthy that Darwin didn't mention competition among females for access to males, nor did he think that males might be choosy. In his book about human evolution, *The Descent of Man*, Darwin (1871, p. 256) makes room for these possibilities when he says that sexual selection "depends on the advantage which certain individuals have over other individuals of the same sex and species solely in respect of reproduction." Darwin's idea that males are "avid" whereas females are "coy" was part of the same stereotype that led him to think that men are more intelligent whereas women are more emotionally sensitive (Hrdy 1997; Bradley 2021).

[7] **Question:** If "natural selection" just means selection that occurs in nature, should artificial selection be regarded as a kind of natural selection?

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Biologists now generally view sexual selection as a kind of natural selection. In sexual selection, males compete with males and females compete with females. In each case, one sex is part of the environment that influences the evolution of traits in the other. It is facts about peahens that caused peacocks to evolve gaudy tails, and it is facts about female elephant seals that cause males to be so much larger than females.[8] Much of natural selection isn't like this – consider the example of a bear species evolving thicker fur as a response to climate change, not as a response to what members of the opposite sex are doing. Although sexual selection frequently results in a polymorphism (meaning that different individuals in the same species have different traits), non-sexual natural selection can do the same thing; I'll describe an example in Chapter 3.[9]

Another feature of Darwin's conception of natural selection is that it occurs on two different levels of organization. The first level involves individual selection, wherein organisms in the same species compete with each other. Group selection occurs when groups of conspecific organisms compete. Darwin introduced the idea of group selection because he saw that there are traits in nature that would be inexplicable if individual selection were the whole story. For example, consider what he says about the honeybee's barbed stinger (Figure 1.3):

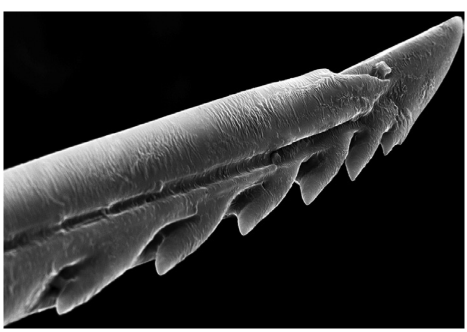

Figure 1.3 The honeybee's barbed stinger.
Source: I thank Rose-Lynn Fisher for permission to reprint "Sting 650x," a scanning electron micrograph from her book *Bee* (Princeton Architectural Press, 2012).

[8] I'll describe an example of sexual selection in dung flies impacting both sexes in Section 8.5. Here females are more "avid" than males.

[9] Sexual selection, as I have defined it, does not explain why organisms reproduce sexually; rather, it presupposes that they do.

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> Can we consider the sting of the wasp or the bee as perfect, which, when used against many attacking animals, cannot be withdrawn, owing to the backward serratures, and so inevitably causes the death of the insect by tearing out its viscera?
>
> If we look at the sting of the bee, as having originally existed in a remote progenitor as a boring and serrated instrument, like that in so many members of the same great order, and which has been modified but not perfected for its present purpose, with the poison originally adapted to cause galls subsequently intensified, we can perhaps understand how it is that the use of the sting should so often cause the insect's own death: for if on the whole the power of stinging be useful to the community, it will fulfill all the requirements of natural selection, though it may cause the death of some few members (Darwin 1859, p. 202).

Bees with barbed stingers die when they sting an intruder to the nest, whereas bees with barbless stingers can withdraw their stingers without harming themselves. The barb is bad for the organism, but it is good for the group, since the barb keeps the stinger in place while it continues to pump venom after the bee has died. Groups of bees that contain individuals with barbed stingers do better at avoiding extinction and at founding new groups than groups that contain individuals with barbless stingers.

Darwin's idea of there being two levels of selection (or "units of selection") was standard during the first half of the twentieth century, but it came in for strenuous attack in the 1960s. To this day, some evolutionary biologists think that hypotheses of group selection are worse than false – they are confused and should be excluded from the toolkit of serious science – whereas other biologists now think that group selection is a coherent hypothesis, the plausibility of which needs to be evaluated on a case-by-case basis. This controversy is the subject of Chapter 3.

1.6 Heredity

For natural selection to cause the frequencies of traits in a population to change, there needs to be heredity. As mentioned, Darwin didn't know about Mendelian genes. After publishing the *Origin*, Darwin advanced his "provisional theory of pangenesis" in his 1868 book *The Variation of Animals and Plants under Domestication*. Luckily for Darwin he did not put that theory in the *Origin*; it is full of holes. What he included instead was a very modest idea, which he called

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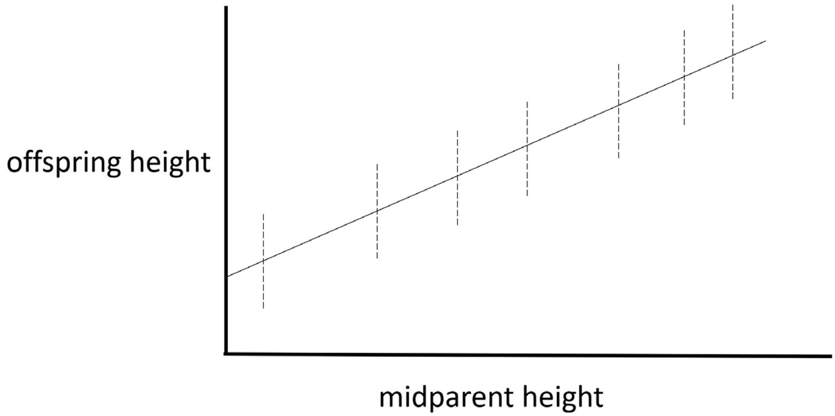

Figure 1.4 Broken lines represent the heights of parents and the heights of offspring associated with different parental pairs. The solid line represents the average offspring heights associated with different midparent heights.

> **The Strong Principle of Inheritance**: Offspring tend to resemble their parents. (Darwin 1859, pp. 5, 127, 438)

This principle does not describe a mechanism whereby parents influence the traits of their offspring. It just says (for example) that taller than average parents tend to have taller than average offspring, as depicted in Figure 1.4. The word "tends" indicates a probabilistic relationship between parents and offspring.[10]

Darwin's silence in the *Origin* about the mechanism of inheritance did not prevent his critics from noting a big problem that his theory confronted – the problem of blending inheritance. For example, suppose that each of the organisms in a population can extract 30 percent of the nutrients that are in the food they eat, and then by chance an advantageous characteristic appears in the population that permits its bearer to extract 90 percent. Darwin would want to show that natural selection can increase the frequency of this new trait so that, some generations hence, everyone extracts 90 percent. The problem is that this won't happen if there is blending inheritance. For example, suppose that when the novel 90-percenter mates with a 30-percenter, their offspring will be able to extract 60 percent. When one of those 60-percenters mates with a 30-percenter, their offspring will be a 45-percenter. After numerous further generations, the novel trait

[10] I'll introduce the concept of mathematical expectation in Section 2.2; it can be used to characterize the probabilistic tendency depicted in Figure 1.4 more precisely.

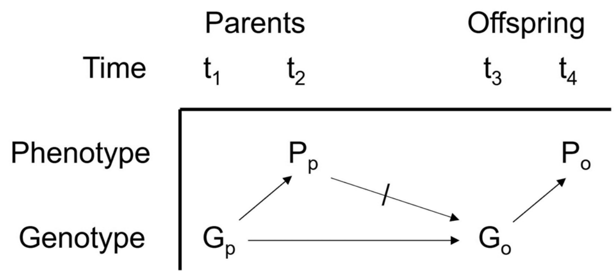

Figure 1.5 The classic Mendelian representation of development and reproduction.

will have been "diluted" to such an extent that the population will not have evolved at all. Fleeming Jenkin (1867) made this objection and it hit home. The problem was solved only after Mendel's ideas were rediscovered in the twentieth century and then integrated with Darwinian natural selection in what came to be called the *Modern Synthesis*. Mendelian genes need not blend in their phenotypic effects; it is perfectly possible that the mating of a 90-percenter with a 30-percenter should result in offspring that are all 90-percenters; this is what dominant genes do.

Mendelian genetics solved one problem for Darwin's theory, but it created another. Mendelism led to the rejection of a second principle about inheritance that Darwin endorsed. He called it

> **The Principle of Use and Disuse**: A trait acquired by a parent may be inherited from that parent by its offspring. (Darwin 1859, pp. 11, 43, 134–155, 143, 168, 447, 455, 472–473, 479–480)

Here Darwin and Lamarck were on the same page. For example, they believed that when blacksmiths working at the forge acquire big muscles, the result will be that their children have big muscles even when they do not exercise. Now the standard evolutionary view is to reject this idea by invoking the Mendelian distinction between genotype and phenotype; see Figure 1.5. The unslashed arrows represent causality, and the arrow with a slash through it denies that there is a causal connection between parental phenotype and offspring genotype.[11]

[11] Figure 1.5 fails to represent the effect of the environment on phenotype, but biologists recognize that phenotypes are almost always influenced by both genes and environment. Ignoring or denying the role of the environment is often called "genetic determinism"; it is often ridiculed, but it is sometimes a useful idealization.

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Biologists often trace this Mendelian picture back to August Weismann (1892) and call it "Weismannism." In fact, Weismann didn't fully embrace Mendelism, but he totally rejected the inheritance of acquired characteristics (which he called "Lamarckism"). Weismann formulated his idea by describing two types of cell that are found in multi-cellular organisms – germ cells and somatic cells. Germ cells are found only in gametes; all the other cells in the organism's body are somatic. What parents transmit to offspring in reproduction is their germ cells, not their somatic cells, and changes in an organism's soma don't change what's in that organism's germ cells.[12]

1.7 Gradualism

Another feature of Darwin's theory that survived well into the twentieth century and still is endorsed by many biologists is his

> **Gradualism**: Evolution almost always occurs by the accumulation of a large number of small changes, not by the accumulation of a small number of large changes.

Darwin was influenced by the gradualist geology that he learned from his Cambridge teacher Charles Lyell, whose 1809 book accompanied Darwin on the Beagle voyage (Hodge 1987; Mayr 2007). However, Darwin felt the pull of a much more general idea. At the end of the *Origin*, Darwin (1859, p. 471) expresses confidence in the general principle that "*Natura non facit saltum* [nature does not make jumps], which every fresh addition to our knowledge tends to make more strictly correct." A third source for his gradualism was his detailed understanding of how plant and animal breeders do their work. In *Variation of Animals and Plants under Domestication*, Darwin (1868, p. 414) describes several varieties "that suddenly appeared in nearly the same state as we now see them," but adds that the overwhelming majority "were formed by a slow process of improvement." Darwin (1868, pp. 234–235) explains this pattern as follows: "As conspicuous deviations of structure occur rarely, the improvement of each breed is generally the result … of the selection of slight individual differences." In another passage, Darwin is

[12] **Question:** Does epigenetic inheritance contradict the Weismann doctrine depicted in Figure 1.5?

less cautious: "Slight individual differences … suffice for [both artificial and natural selection], and are probably the sole differences which are effective in the production of new species" (p. 192). Darwin's gradualism was "the received view" for most of the twentieth century, but population geneticists have found flaws in an influential argument that defends that thesis. This change isn't widely known in the rest of evolutionary biology, let alone among philosophers of biology. It's time for an update, which I'll describe in Chapter 6.

1.8 Mutation

Darwin's gradualism concerns the mutations that are apt to increase in frequency in populations once they occur. This raises the question of why mutations occur in the first place. Darwin's answer remains a pillar in modern evolutionary theory:

> **Mutations are random:** Mutations have their causes, but they do not occur because they would be useful to the organisms in which they occur.

In *Variation of Animals and Plants under Domestication*, Darwin (1868, pp. 248–249) explains this thesis by presenting a beautiful analogy:

> Let an architect be compelled to build an edifice with uncut stones, fallen from a precipice. The shape of each fragment may be called accidental; yet the shape of each has been determined by the force of gravity, the nature of the rock, and the slope of the precipice, – events and circumstances all of which depend on natural laws; but there is no relation between these laws and the purpose for which each fragment is used by the builder. In the same manner the variations of each creature are determined by fixed and immutable laws; but these bear no relation to the living structure which is slowly built up through the power of selection whether this be natural or artificial selection.

I'll discuss the meaning and justification of the thesis that mutations are random in Chapter 6.

Darwin thought that natural selection and mutation have something in common. He says in his *Autobiography* (1958, p. 50) that "there seems to be no more design in the variability of organic beings and in the action of natural selection, than in the course which the wind blows." This similarity sits side by side with a difference: Mutations do not arise because they are useful, but variants that exist in a population increase in frequency because they are useful. In both cases, the processes can and do occur without guidance from an intelligent designer.

1.9 Was Darwin "Illogical"?

In his essay "Darwin's Five Theories," Mayr (2007, pp. 97–98) says that Darwin was "illogical" because he failed to recognize that his theory was in fact five distinct theories that are logically independent of each other.[13] For Mayr, this was no small failing; he says that "Darwin's blindness to recognize this [logical independence] became one of the main reasons for the never-ending controversies on evolutionary biology after 1859." Here's how Mayr separates the parts of the Darwinian picture:

(1) evolution as such
(2) common descent
(3) gradualism
(4) multiplication of species
(5) natural selection

Although Mayr is sometimes unclear about which propositions he wants these phrases to denote,[14] his list does correspond significantly to the parts of Darwin's theory that I've described in this chapter.

I have two beefs with Mayr's charge of illogicality. First, a slightly enriched representation of Darwin's theory shows that there are logical dependencies among its elements. I noted earlier that common ancestry, conjoined with the observation that current species differ in their inherited characteristics, entails that evolution must have occurred, and that

[13] Proposition A is logically independent of proposition B precisely when the four conjunctions A&B, A&notB, notA&B, and notA&notB are all logically possible, meaning that none of them is a contradiction. Probabilistic independence is different from logical independence, as I'll explain in Chapter 6.

[14] For example, here is how Mayr (2007, p. 100) characterizes common descent: "every group of organisms descended from an ancestral species." What does Mayr mean by "group"? If the totality of organisms alive today doesn't count as a "group," Mayr's formulation fails to capture the idea of *universal* common ancestry. **Question:** "Everyone has a birthday" does not entail that there is a single day on which everyone was born. To think otherwise is to commit what I call "the birthday fallacy" (Sober 1990, pp. 42–43). How does this point apply to Mayr's characterization of common descent?

universal common ancestry entails that there were no "walls" that prevented one species from evolving into another. In Chapter 7, I'll describe how Darwin and his successors have used the fact of common ancestor to reconstruct the character states of ancestors; without common ancestry, the character states of ancestors would have been purely conjectural, as witnessed by Lamarck's theory that evolution pushes lineage to evolve from simpler to complex. In Chapter 8, I'll describe how Darwin used the idea of common ancestry to refute some seemingly plausible hypotheses about natural selection.

Second, I think that Darwin clearly saw that there are parts of his theory that are logically independent of each other. For example, he recognized the separateness of evolution and universal common ancestry. Darwin was aware that Lamarck's theory embraced the former while denying the latter. Darwin disliked Lamarck's theory, but he never accused it of being logically contradictory. Another example of Darwin's logical lucidity can be found in his discussion of the evidence that supports the different parts of his theory. Darwin (1859, p. 427) argued that neutral and deleterious similarities provide telling evidence for common ancestry, whereas adaptive similarities do not. The fact that dolphins and sharks are both shaped like torpedoes isn't strong evidence that they have a common ancestor, since one would expect large aquatic predators to evolve that shape even if they lacked a common ancestor. On the other hand, the fact that humans and monkeys both have tailbones is strong evidence for their common ancestry, since tailbones are useless to humans. Darwin's thoughts here, which I'll analyze in Chapter 4, show that he realized that common ancestry and natural selection are logically independent.

Mayr was right to separate the logically independent propositions in Darwin's theory, but their logical independence does not mean that they are mutually irrelevant. One of my goals in what follows is to show how the parts of the theory fit together. In tracing out these connections, I'll make use of ideas from modern evolutionary theory of which Darwin never dreamt.