Plant Evolution

An Introduction to the History of Life

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CONTENTS

Introduction

> The unpredictable and the predetermined unfold together to make
> everything the way it is. It's how nature creates itself, on every scale,
> the snowflake and the snowstorm.
> —TOM STOPPARD, *Arcadia*, Act 1, Scene 4 (1993)

Much has been written about evolution from the perspective of the
history and biology of animals, but significantly less has been writ-
ten about the evolutionary biology of plants. Zoocentricism in the
biological literature is understandable to some extent because we are
after all animals and not plants and because our self-interest is not
entirely egotistical, since no biologist can deny the fact that animals
have played significant and important roles as the actors on the stage
of evolution come and go. The nearly romantic fascination with di-
nosaurs and what caused their extinction is understandable, even
though we should be equally fascinated with the monarchs of the
Carboniferous, the tree lycopods and calamites, and with what caused
their extinction (fig. 0.1). Yet, it must be understood that plants are
as fascinating as animals, and that they are just as important to the
study of biology in general and to understanding evolutionary theory
in particular. Consider, for example, that the fossil remains of the tree

Figure 0.1. A suggested reconstruction of the Carboniferous (359–300 Mya) flora dominated by tree-sized (arborescent) lycopods such as *Lepidodendron* (right foreground) and arborescent calamites such as *Calamites* (left rear). This type of vegetation grew in geographically expansive, swampy environments throughout Europe and North America. Its fossil remains constitute most of today's commercial grade coal. The extinction of the Euramerican lepidodendrids and calamites toward the end of the Westphalian stage of the Carboniferous (~312–299 Mya) is attributed to climate changes and to tectonic activity that reduced the geographical expanse of the coal-swamp ecosystems. Courtesy of The Volk und Wissen Volkseigener Verlag, Berlin.

Table O.1. Formal and informal names of some of the living plant groups mentioned in the text

Prokaryota (polyphyletic)

    Eubacteria
    Archaea

Eukaryota (eukaryotes)

    algae (polyphyletic)

        Class Charophyceae (charophytes)[a]
        Class Chlorophyceae (green algae)[a]
        Class Phaeophyceae (brown algae)
        Class Rhodophyta (red algae)

    Embryophyta (monophyletic) [a]

        bryophytes (paraphyletic)

            Phylum Bryophyta (mosses)
            Phylum Marchantiophyta (liverworts)
            Phylum Anthocerotophyta (hornworts)

        vascular plants/tracheophytes

          seedless vascular plants

            Phylum Lycopodiophyta (lycopods)
            Phylum Monilophyta (ferns and horsetails)[b]

          seed plants

            gymnosperms (polyphyletic)

            Phylum Cycadophyta (cycads)
            Phylum Ginkgophyta (*Ginkgo*)
            Phylum Coniferophyta (conifers)
            Phylum Gnetophyta (gnetophytes)

           Flowering plants (monophyletic)

            Phylum Anthophyta (angiosperms)

[a] The green algae (Chlorophyceae and Charophyceae) and the Embryophyta are a monophyletic group of plants that are collectively called the Viridiplantae. The Charophyceae and the Embryophyta are collectively referred to as streptophytes.

[b] Although the monilophytes have been given formal taxonomic status and evolved from a last common ancestor (trimerophytes), the horsetails evolved independently from the ferns, and there is ample evidence that modern-day ferns had independent origins. Thus, the monilophytes should be considered a paraphyletic group of plants.
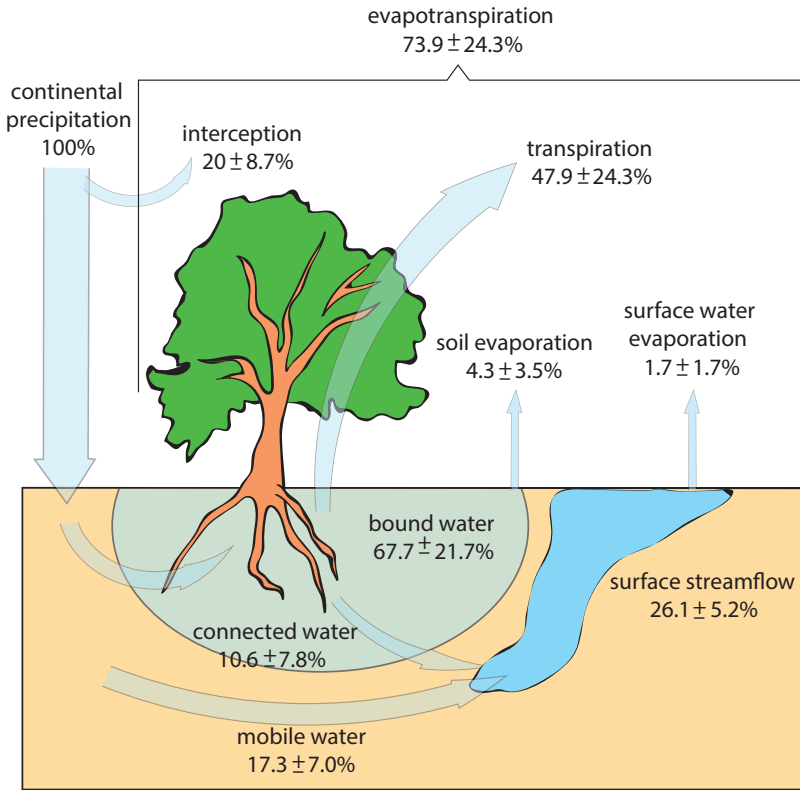
Figure 0.2. Schematic of global hydrological fluxes (expressed as percentages of continental precipitation, 100%) based on a model using isotopic data and estimates of terrestrial plant gross primary productivity. The model assumes that plants lose ~300 water molecules per CO_2 fixed by photosynthesis, which predicts that plant transpiration equals 55,000 kn³/yr., and that gross primary productivity equals ~120 Pg C/yr. Note that one petagram (Pg) equals 10^{15} grams, or one billion metric tons. Note further that transpiration accounts for ~47.8% of the total continental precipitation, which is ~65% of total evapotranspiration. These data emphasize the important roles land plants play in influencing Earth's hydrological cycles that in turn influence the movement of nutrients and soil contaminants. The schematic is based on data reported by Good, Noone, and Bowen (2015).

lycopods and tree horsetails produced much of the coal that fueled the early days of the industrial revolution (table 0.1). Consider also how important plants are to the Earth's ecosystem (fig. 0.2).

The introduction to a book about evolution can serve many purposes as for example to disabuse the notion that evolution has di-

rectionality or purpose, which is a common misconception that can lead to heated debates where none should exist. Nevertheless, the misconception emerges for a number of reasons. Clearly, time has direction, and the fossil record preserves the long history of evolution in chronological order that reveals many clear-cut trends as for example a trend toward increasing body size in some, but not all, lineages. Likewise, our species has a predilection for pareidolia—the tendency to see patterns where none exist, as for example "the man in the moon." However, none of these phenomena justify the assumption that evolution has a prefigured pattern, or some sort of goal. Evolution must abide by many rules, but these are prefigured in the laws of physics and chemistry, and the overarching laws of chance.

Why Study Plants?

But first, why study plants? The next time you walk through a forest, park, or garden, consider how alike and yet unalike you are from the plants that surround you. You and they are made of cells, each of which contains organelles called mitochondria that consume oxygen to power cellular metabolism. Like plants, our cells also contain copies of the remarkable molecule called DNA (deoxyribonucleic acid) that contains most, albeit not all, of the information needed to keep you alive. Perhaps even more astounding is the fact that we and every plant around us are distantly related, albeit at a time when life first started to evolve billions of years ago. As surmised by Charles Darwin (1809–1882), all forms of life are related because, with the exception of the very first living things, organisms can evolve only from preexisting organisms. To be specific, Darwin vigorously proposed and defended five propositions in his magnum opus, *On the Origin of Species*:

(1) All life evolved from one or a very few simple, unicellular organisms.
(2) All subsequent species evolve from preexisting species.
(3) The greater the similarities between taxa, the more closely they

are related to one another and the shorter their evolutionary divergence times.

(4) The process giving rise to species is gradual and of long duration.

(5) Higher taxa (genera, families, etc.) evolve by the same evolutionary mechanisms as those that give rise to new species.

As we will see throughout this book, propositions (4) and (5) are problematic for certain species and some higher taxa. However, propositions (1)–(3) have received extensive experimental validation, both in terms of molecular analyses and classical comparative anatomy and morphology. There is no doubt that each of us is related to every other living thing as a consequence of uncountable ancestor-descendant relationships comprising a genealogy that extends back to the dawn of life.

Yet, consider too that we are very unlike plants. Most of our cells are held together primarily by glycoproteins called cadherins, whereas most of the cells in land plants are held together with the help of multifunctional pectic polysaccharides. Likewise, with only a few exceptions, plant cells have cell walls that provide mechanical support by virtue of one of the strongest naturally occurring polymers on the planet, cellulose. In addition, green plant cells contain organelles called chloroplasts that, in the presence of sunlight, convert carbon dioxide, water, and a few essential elements into new living cells. Astronomers like to tell us that we are made of stardust—because the elements in our bodies were fabricated in the hearts of stars now long vanished from the night's sky. If this is true, it must also be said that we are made of starlight—because plants provide all animals, either directly or indirectly, with food thanks to the evolution of a process called photosynthesis.

Even if plants were not the foundation of almost every food chain on our planet, they deserve our unwavering attention because they have done far more than feed the world over the course of evolutionary history. Consider two facts. Most extant organisms require oxygen to live. Yet, Earth's first atmosphere lacked oxygen. Indeed, oxygen was probably toxic to many of the first forms of life on this
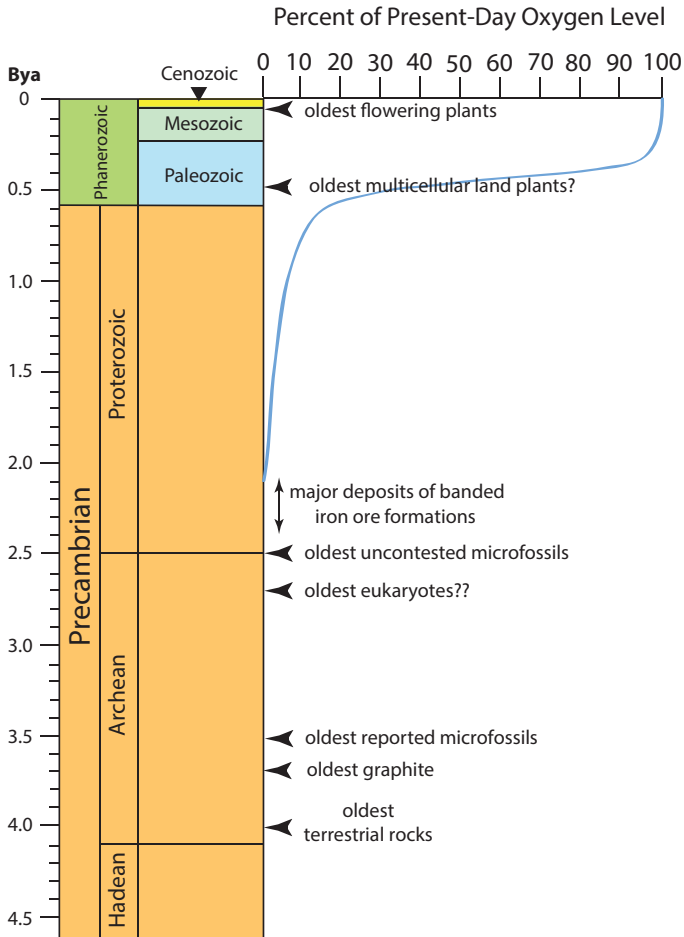
Figure 0.3. Estimates of the percent of present-day levels of atmospheric oxygen (100% denotes current oxygen level) plotted as a function of geological time (in billions of years before present). A few evolutionarily important events, such as the appearance of the first cells containing organelles (eukaryotic cells), are concurrently plotted. The horizontal line measures our uncertainty about the precise timing of each of these events.

planet. So, how did the majority of organisms come to require oxygen? The answer requires knowing that plant photosynthesis splits water molecules and releases oxygen. Once this metabolic process evolved, Earth's atmosphere changed from one composed of methane, ammonia, carbon monoxide, and other reducing gases into an oxidizing atmosphere like the one we breathe today (fig. 0.3). The evidence for

Table 0.2. Six examples of how plant evolution changed the physical and biological world

(1) Evolution of Photosynthesis	→	Transformed a reducing atmosphere into an oxidizing atmosphere; provided heterotrophs food.
(2) Evolution of Land Plants	→	Ameliorated the terrestrial landscape; paved the way for the colonization of the land by animals; shaped water and nutrient soil cycles.
(3) Evolution of Wood	→	Sequestered carbon dioxide; provided light-weight building material that amplified the three-dimensionality of terrestrial communities; shaped ecosystems by virtue of forest fires.
(4) Evolution of Flowering Plants and Endosperm[a]	→	Permitted the storage of seeds by early humans thereby fostering the transition from a hunting-gathering society to an agrarian society.
(5) Fossilization of Plants and Coal Formation	→	Fostered the Industrial Revolution.
(6) Diversification of Secondary Plant Metabolic Products	→	Continues to provide numerous pharmaceuticals.

[a] Endosperm is a specialized tissue produced in the developing seeds of flowering plants. It provides nutrients to the developing embryo within the seed, which typically dehydrates and undergoes a dormancy period. This developmental pattern allows seeds to be dried and stored for long periods.

this claim is extensive and will be presented in greater detail when we discuss the origin and early evolution of life (see chapter 1). For now, it is sufficient to recognize that the evolution of plants has literally changed the world (table 0.2), and that no one can claim to understand evolution unless they understand plant biology.

What Does Evolution Mean?

But what is evolution? What does the word really mean? To be sure, definitions of complex things are difficult to construct in ways that are acceptable to everyone. This generalization holds true for the concept of evolution, which helps to explain why different authors have defined

Figure 0.4. Sassafras leaves taken from the same branch illustrate phenotypic plasticity. The differences in shape result from developmental responses to the effects of gravity on developing leaves. Leaves developing on the upper sides of branches tend to be unlobed. Leaves developing on the sides of branches tend to be mitten shaped. Leaves developing on the lower sides of branches tend to have three lobes.

evolution in slightly different ways. Yet, most definitions adopt the phrase *descent with modification* or contain language that says much the same thing. Evolution is a record of the heritable changes in the characteristics (traits) of organisms over a few or many generations. Notice that this definition does not speak to *how* evolution occurs. Rather, it merely *describes* a process. Also notice the use of the word *heritable*. The changes that occur across successive generations must be the result of genomic modifications and not the result of developmentally reversible responses of individual organisms to their environmental conditions. The leaves developing on the same branch of a tree can differ in size, shape, or other traits in response to differences in light or the effects of gravity (fig. 0.4). The capacity for this developmental plasticity is an inherited feature, and it is nowhere better expressed than in sedentary organisms like the land plants who must continue to grow in one place where environmental conditions can change, often dramatically over the course of a few or many years. However, the

particular differences among individual leaves growing in the sun or in the shade are not inherited traits that can be passed down to the next generation a tree produces. If they were, each tree would be capable of producing leaves of only one shape and size. Rather, leaves differing in shape but drawn from the same plant illustrate that a single genotype (the combined genome of an organism, which in the case of plants includes the genetic information stored in the nucleus, mitochondria, and chloroplasts) can produce different phenotypes (the physical manifestation of all of an organism's traits) in response to different environmental conditions. Consequently, the word evolution is not applied to changes in an individual organism, but rather to modifications in the traits of descendants with respect to ancestral traits.

As mentioned earlier, a regrettable misconception about evolution is that it has purpose—some grand design. This misconception rests in part on the notion that heritable changes cannot revert back to the ancestral condition. Yet, this is demonstrably wrong—evolution does not have a prefigured direction and reversals are not uncommon as for example the evolution of vestigial leaves in the relatives of plants that possessed large leaves (as for example, the leaves of the herbaceous horsetail *Equisetum* and the arborescent horsetail *Calamites*; fig. 0.5). Reduction is particularly evident in instances of the evolution of parasitism as for example the Indian Pipe (*Monotropa uniflora*), which has highly reduced, nonphotosynthetic leaves (fig. 0.6).

Nevertheless, most biologists agree on the existence of major evolutionary transitions that have collectively established what appear to be trends in the fossil record. For example, prebiotic replicating molecules preceded the appearance of membrane-bound protocells in which originally independent genes subsequently became aggregated into chromosomes (table 0.3). Yet, at finer levels of resolution, each of these transitions must be seen as the statistical summation of numerous smaller events, some of which involved gains, losses, or reversals of previous events. For example, depending on the group of organisms (or the time interval) examined, body size may increase or decrease in

Figure 0.5. Comparison of the vestigial leaves of the horsetail (*Equisetum*) shown on the left panel and the larger leaves of the organ genus for the leafy shoots of the tree-sized calamites (*Annularia*) shown on the right panel (scale is in millimeters). The leaves of the horsetail are highly reduced in size and fused together along their margins to form a crown-like whorl. Only their tips are individually recognizable, both on main and lateral branches (arrows). Unlike the leaves shown here, most mature horsetail leaves are not photosynthetically functional. The leaves of calamites were likewise arranged in a whorl, but they were unfused at their margins, larger, and photosynthetic.

the fossil record of a particular lineage just as the degree of ecological specialization may increase or decrease over the long course of the history of a lineage or clade. Consequently, claims for the existence of evolutionary trends depend on our particular taxonomic and temporal foci. Indeed, in a very real sense, what appear to be broad patterns in evolutionary history are fractal-like in the sense that their existence depends on our scale of measurement (much like the length of a coast-line depends on the length of the yardstick used to measure it).

Figure 0.6. Colorless flowers and vestigial leaves (left) and developing fruits (right) of the Indian Pipe (*Monotropa uniflora*), a parasitic angiosperm placed in the Blueberry family (Ericaceae).

Table 0.3. Six examples of evolutionary transitions (in approximate chronological order of occurrence; top to bottom) that collectively appear to constitute an evolutionary trend of increasing complexity

(1) Replicating Molecules	→	Compartmentalized Replicating Molecules
(2) Independent Genes	→	Chromosomes
(3) Unicellular Prokaryotes	→	Multicellular Prokaryotes
(4) Multicellular Prokaryotes	→	Cellular Specialization
(5) Unicellular Eukaryotes	→	Multicellular Eukaryotes
(6) Aquatic Multicellularity	→	Terrestrial Multicellularity

Patterns and Trends

The coastline-yardstick analogy helps us to understand why the interpretation of some patterns in the fossil record has proven contentious. Consider the contrasting perspectives of Christian De Duve (1917–2013) and Stephen Jay Gould (1941–2002). De Duve observes a clear directionality in a trend going from functionally general and inefficient biochemical reactions to progressively more specific and

efficient reactions during the molecular transition from an abiotic to a biotic world. According to this view, evolutionary patterns emerge from orderly molecular modifications and adaptive innovations that translate ultimately into complex molecules such as DNA. Gould also sees patterns in life's macroscopic history, but argues that most are largely the result of unpredictable contingent events ranging from developmental quirks early in the ontogeny of ancestral organisms carried forth into their descendants to global catastrophes such as the asteroid collision that resulted in the Cretaceous-Paleogene mass extinction (also called the K-T event; see fig. 9.19). However, these two worldviews arise because De Duve and Gould are viewing different coastlines and using very different yardsticks with which to measure it. De Duve's coastline is constructed by the unalterable laws of physics and chemistry. His yardstick is a molecule. Gould's coastline is constructed out of macroscopic morphological transformations preserved in the fossil record. His yardstick is the observable phenotype. De Duve sees patterns because of predictable molecular verities. Gould sees patterns resulting from seemingly random historical events that are refined subsequently by the operation of natural selection. Both worldviews are real, but the two are very different. One emerges from necessity. The other comes largely from chance.

Necessity and Chance

The tension between necessity and chance lies at the heart of many aspects of biology, but none more so than in evolutionary biology because of the roles played by selection and genomic variation. Physics certainly encompasses the determinism of classical Newtonian mechanics (which describes the behavior of billiard balls and planets) and the randomness of quantum mechanics (which describes the behavior of quarks and electrons). However, these two contrasting paradigms operate at such different physical scales that one paradigm rarely affects the other in ways perceptible to us. This does not hold true when we examine classical Darwinian evolutionary dynamics. Consider the

theory of natural selection as proposed independently by Charles Dar-
win and Alfred Russel Wallace (1823–1913), which makes five major
assertions:

(1) The number of individuals in a population should increase
    geometrically.
(2) However, the number of individuals tends to remain constant.
(3) Therefore, only a fraction of the offspring that are produced
    survive because the environment provides limited resources.
(4) Those offspring that survive and reproduce differ from those
    that die because the individuals in a population differ owing to
    heritable variation; and
(5) the struggle to survive and reproduce determines which variants
    will perpetuate the species.

According to this theory, the *necessity* of natural selection results
in the accumulation of favorable heritable traits in successive gener-
ations by means of the elimination of individuals bearing traits that
are less favorable to survival and reproductive success. The result is a
macroscopic evolutionary pattern that can appear to have direction
(and, to some people, even design and purpose).

However, heritable differences in traits are the result of chance
molecular changes in an organism's genome, changes that result from
spontaneous random mutations (table 0.4), or from genetic recom-
bination during meiosis and sexual reproduction (fig. 0.7). Most mu-
tations are lethal, or at best neutral, in their effects. Those that are
not lethal introduce heritable changes in the next generation without
the benefit of sexual reproduction. Genetic recombination results as
a consequence of chromosome pairing and crossing-over during mei-
osis, a process that will be described in detail in chapter 3. To be very
clear, organisms have evolved extremely sophisticated mechanisms
to proofread their DNA and repair or purge modifications from their
genomes. Likewise, mutations and crossing-over do not occur with
equal probability throughout an organism's genome. Some DNA se-

Table 0.4. Examples of mutations that alter DNA sequences and thus protein function

(1) Deletion	The removal of DNA nucleobases,[a] e.g., CTGGAG → CTGGA.
(2) Duplication	The formation of a DNA sequence that is copied more than one time.
(3) Insertion	The addition of DNA nucleobases, e.g., CTGGA → CTGGAT.
(4) Frameshift mutation	A deletion or insertion of one or more DNA nucleobases that shifts the type(s) of amino acid(s) encoded for a protein, for example The Fat Cat Ate Fat → heF atC atA teF at.
(5) Missense (substitution) mutation	A change in one DNA nucleobase triplet that results in the substitution of one amino acid for another amino acid in a protein sequence, e.g., GAG→GTG in the β-globin gene results in sickle cell anemia.
(6) Nonsense mutation	A change in one DNA nucleobase pair that truncates protein construction and results in a shortened protein.
(7) Repeat expansion	Short DNA sequences that are repeated one or more times in a row, e.g., CTGGAG → CTGGAG CTGGAG CTGGAG.

[a] The four DNA nucleobases are adenine (A), cytosine (C), thymine (T), and guanine (G).

quences are more prone to mutation and crossing-over, while others are not. Consequently, in this context, the word chance does not mean random.

Nevertheless, mutations and recombination involve elements of chance. Mutations are random in the sense that an organism cannot instigate or specify what part of its genome will mutate or what a mutation will produce. Likewise, with the exception of human medical intervention, an organism has no direct control over which sperm cell will fertilize a particular egg. Viewed in the most simplistic of ways, mutations and genetic recombination are genomic accidents that provide the heritable variation that opens the possibility that selection will subsequently influence which variants die and which prosper.

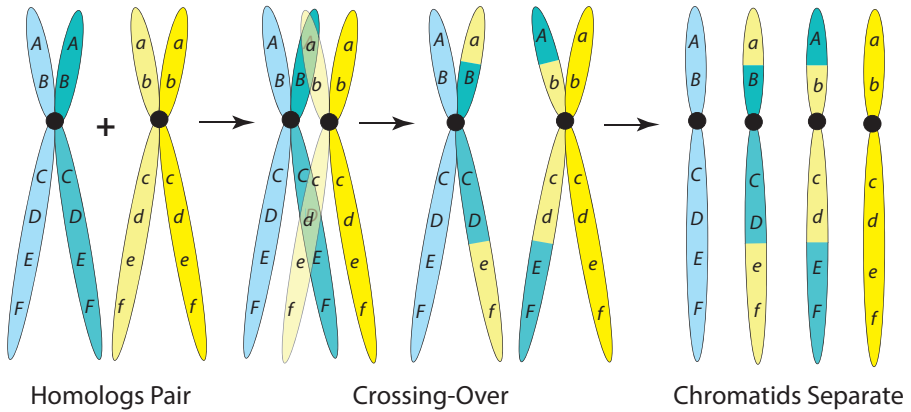It is important to not lose sight of one of the great insights pro-

Homologs Pair   Crossing-Over   Chromatids Separate

Figure 0.7. Genetic recombination results in progeny with combinations of genetic infor-
mation differing from those of either parent. It is the result of genetic materials shuffled
between parents when sperm and egg fuse to form a zygote and from a phenomenon
called crossing-over wherein homologous chromosomes (homologs), each consisting of
two chromatids (here shown in different shades of blue and different shades of yellow)
pair during meiosis (to produce sperm or egg) and transmit physical portions from one
chromatid to the corresponding portions of the other chromatid (diagrammed from left to
right). In the process sister chromatids will differ in allelic forms of genes (shown as a series
of letters; dominant alleles in capitals and recessive alleles in lower cases). The chromatids
of each chromosome are separated during meiosis to produce four chromosomes that in
this case differ in each of their genetic makeup. The exchange of genetic information need
not involve chromosome breakage; it can result from the transfer of copies of portions of
chromosomes (not shown).

vided by the Darwin-Wallace theory of natural selection—an insight
that significantly colors our perception of what we mean when we
speak of adaptation. Correlated variables have meaning only in re-
lation to one another such that one variable cannot be conceived of
as cause or effect. This is a subtle but profoundly important insight.
Organisms evolve, and by doing so they change their environments.
Reciprocally, when environments change, organisms must evolve if
they are to survive and reproduce successfully. This reciprocity drives
a process that gives the appearance of progress because competition
among individuals necessitates adaptive invention and novelty, or
extinction. The theory of natural selection tells us that each species
must either evolve to survive the gauntlet of changing environmental
conditions, or suffer and ultimately perish. The fossil record also tells

us that the end game of evolution is death. Well over ninety percent of all previous forms of life are extinct. This gruesome statistic shows that adaptions are never perfect. They are only temporarily effective.

Mendel, Planck, and Particulate Heredity

The theory of natural selection goes a long way to explain *why* organisms evolve, but it is silent about *how* they evolve. Charles Darwin mustered a remarkable amount of evidence for the physical manifestations of evolution, but he was unaware of hereditary mechanisms, including mutation and recombination. Darwin was remarkably clear about this. In his chapter on the "Laws of variation" (Darwin 1859, p. 170), he writes, "Whatever the cause may be of each slight difference in the offspring from their parents—and a cause for each must exist—it is the steady accumulation, through Natural Selection, of such differences, when beneficial to the individual, that give rise to all the more important modifications of structure, by which the innumerable beings on the face of this earth are enabled to struggle with each other, and the best adapted to survive." At the beginning of the same chapter (1859, p. 131), Darwin states that variation is "due to chance," but he goes on to say, "This, of course, is a wholly incorrect expression, but it serves to acknowledge plainly our ignorance of the cause of each particular variation." In this context, it is fair to say that the word chance has often been used to explain what we do not know or cannot explain.

This huge gap in knowing what chance means began to disappear with the rediscovery in 1900 of the seminal work of Gregor Mendel (1822–1884) on particulate inheritance, which was the same year that Max Planck (1858–1947) introduced his concept of quantum discontinuity. Curiously, the theories of Mendel and Planck had one important feature in common—both hypothesize discretized entities, traits in the context of Mendel's heredity theory and quanta in the case of Planck's black-body theory. In order to understand the depth of this coincidence, consider that Mendel selected peas (*Pisum sativum*)

with which to explore heredity for two reasons. First, peas have non-opening, self-pollinating (cleistogamous) flowers, which allows plant breeders to know the source of the pollen used to produce the next generation of seeds, and, second, some of the more easily measured traits exhibited by peas have only two phenotypic states as for example seed color (yellow versus green) and seed shape (smooth versus wrinkled). The pollination syndrome and the "either or" genetics of peas allowed Mendel to discover the laws of inheritance using seven traits: plant height, pod shape and color, seed shape and color, and flower position and color. Over the course of his studies, Mendel discovered that some phenotypes were dominant, whereas others were recessive. For example, when a yellow pea plant is pollinated with pollen from a plant with green peas, all of the peas in the next generation are yellow (thus yellow is dominant, whereas green is recessive). However, in the following generation of plants that were allowed to self-pollinate, green peas reappeared at a ratio of 1:3. A graphical technique, formulated by Reginald Punnett (1875–1967) and named in his honor as Punnett squares, diagrams these relationships efficiently (fig. 0.8).

In contemporary terminology, the molecular domains of DNA that code for a trait are called genes, whereas alternative DNA sequences in the same DNA segment are called alleles (that is, alleles are alternative forms of the same gene). In the foregoing example of Mendelian genetics, the gene for pea color has two allelic forms (yellow and green). Diploid organisms such as peas inherit one allele for each gene from each parent. An individual that has two copies of the same allelic form of a gene (as for example *YY* in fig. 0.8) is said to be homozygous for that gene, whereas an individual that has two different allelic forms of a gene (*Yg* in fig. 0.8) is said to be heterozygous for that gene.

The "Modern Synthesis" That Was Neither Modern nor Synthetic

Unfortunately, Mendel's brilliant insights were not understood by those who initially read his work. Perhaps worse, Mendel's work was
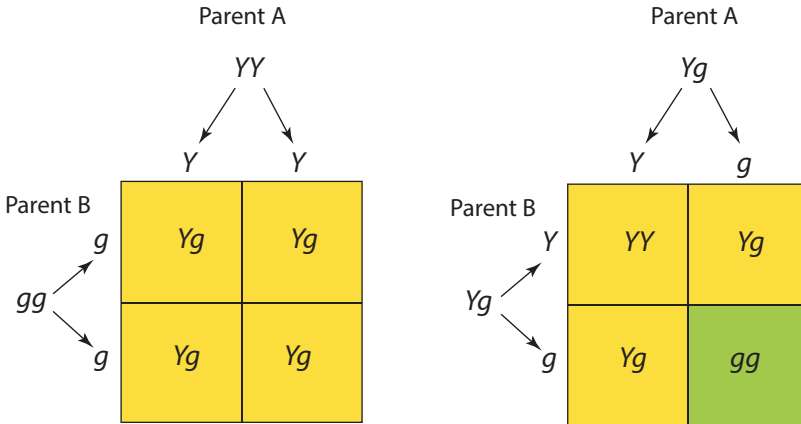
Figure 0.8. Punnett squares illustrating what happens when a yellow pea is crossed with a green pea (left) and when the progeny of this cross are allowed to self-pollinate (right). When a yellow pea (*YY*) is crossed with a green pea (*gg*), all of the progeny are yellow peas (*Y* is dominant), despite the fact that the allele for green is present in each of the four genotypes (*g* is recessive). When the progeny produced by the first cross are allowed to self-pollinate, three genotypes are produced, one of which is homozygous for green (*gg*) and two of which produce the yellow phenotype (one that is homozygous, *YY*, and another that is heterozygous, *Yg*). Statistically, the result is one green phenotype for every three yellow phenotypes (1:3). Note: It is conventional to denote genes in italics and to use upper- and lower-case letters for dominant and recessive genes, respectively.

wholly unknown to Darwin. Had the latter learned of the laws of Mendelian inheritance, genetics might have prospered earlier than it did and Darwin would never have invented pangenesis as a mechanism for inheritance. Fortunately, Mendel's work was independently duplicated and rediscovered by Hugo de Vries (1848–1935) and Carl Correns (1864–1933), both of whom published their work within a two-month period in the spring of 1900. The curious initial result was that biologists quickly accepted Mendel's ideas, but supposed them to be largely incompatible with Darwinian evolution for the simple reason that Darwin's theory emphasized the effects of selection on traits manifesting continuous rather than "either or" variation. In contrast, Mendelian genetics was particulate (either yellow or green, either wrinkled or smooth, etc.) with no intermediates. Notice that the example of Mendelian genetics illustrated in fig. 0.8 can never achieve more than three genotypes (*YY*, *Yg*, and *gg*) and never more than two

seed color phenotypes (yellow and green). Barring some sort of muta-
tion, there are no possible intermediates upon which selection can act
because the genes underlying seed color are qualitative in nature. The
impasse between Darwin's theory and Mendel's theory was resolved
when the existence and behavior of quantitative genes were fully
recognized (box 0.1). Quantitative genes typically act in concert and
result in phenotypic traits that vary by degrees. Quantitative traits,
such as body mass or height, are those that can vary continuously and
that depend on the cumulative actions of more than one gene and
their interaction with the environment.

The comfortable merger of Darwinian evolution with Mendelian

Box 0.1. Quantitative Traits and the Length of Tobacco Corollas

Mendelian genetics was described in the text as "particulate" because the traits origi-
nally studied by Gregor Mendel were discontinuous discrete traits, as for example green
or yellow peas. However, many traits are continuous traits, such as body length or plant
height. These attributes are called quantitative traits, many of which are the result of
the cumulative interactions among two or more genes and interactions among these
genes and the environment. A quantitative trait locus (QTL) is a polygenic portion of
DNA that correlates with and participates with the regulation of the phenotypic variation
in a quantitative trait. Early in the twentieth century, after the rediscovery of Mendel's
work, it was not immediately obvious to geneticists how Mendelian (particulate) genetics
could be reconciled with quantitative traits. The American geneticist William E. Castle
(1867–1962) is generally credited with making the first attempt to reconcile Mendelian
genetics with Darwin's theory of speciation. Castle argued that the appearance of novel
traits complying with Mendelian genetics resulted in new species—that is, the evolution
of new discontinuous traits is the basis for phenotypic discontinuity and thus speciation.
This speculation did not address the mechanisms responsible for QTL. However, it did
help to shift attention to the genetics of QTLs.

One of the early pioneers studying quantitative traits was the American plant ge-
neticist Edward M. East (1879–1938), who studied tobacco and corn. One of his seminal
papers dealt with the inheritance of the style and corolla length of tobacco (*Nicotiana*).
He made crosses between *N. alata grandifolia* and *N. forgetiana*, which differ phenotyp-
ically only in the size and color of their flowers, and measured the lengths of styles and
corollas of the parental plants, their progeny (F_1), and the second generation of plants
(F_2). The mean corolla lengths of these two species were found to differ by more than 53
mm, whereas the frequency distribution of the corolla length of the F_2 generation was
continuous, albeit positively skewed (fig. B.0.1). From these measurements, East devel-

genetics along with the contributions of biometricians, such as Ronald Fisher (1890–1962) and Sewall Wright (1889–1988), lead to what is popularly called the Modern Synthesis. We will examine some of the historical details of this epoch in chapter 3. For now, it is sufficient to enumerate a few of the major concepts that emerged when evolutionary theory was invigorated by the insights of population genetics (table 0.5), and to juxtapose some of these concepts with those of Darwin.

For example, Darwin as well as most of the major contributors to the Modern Synthesis conceived of speciation as a comparatively slow process. However, this is not necessarily always true. Although

oped a genetical model and concluded, "the difference in corolla length shown by these two species [was] represented by the segregation and recombination of four cumulative but independent pairs of unit factors [genes], dominance being absent" and that "the Mendelian notation . . . to describe complex qualitative inheritance . . . is similarly useful in describing the inheritance of quantitative characters." This seminal conclusion set the stage for a true synthesis of genetics and evolutionary theory.
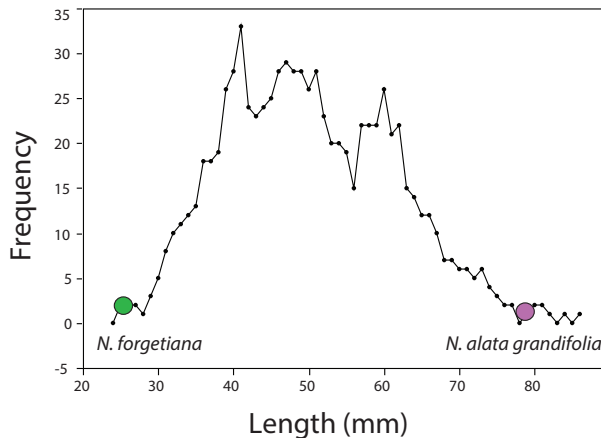

Figure B.0.1. The frequency distribution of the corolla length of the second generation (F_2) crosses between *Nicotiana forgetiana* and *N. alata grandifolia* illustrates what is meant by a quantitative (continuous) trait. The mean corolla length for each of the two parental species is shown as colored circle. Data taken from East (1913).

Table 0.5. Eight major concepts and conclusions characterizing the Modern Synthesis

(1) Evolution is the change of allele frequencies in the gene pool of a population over many generations.
(2) The gene pools of different species are isolated from one another, whereas the gene pool of a species is held together by gene flow.
(3) Each individual of a sexually reproductive species has only a portion of the alleles in the gene pool of its species.
(4) The alleles and allelic combinations of the individual are contributed by two parents (and arise from independent assortment) that may be modified by chromosomal or genic mutations. Mutations are the ultimate source of new alleles and genes.
(5) Individuals favored by natural selection will contribute larger portions of their genes or gene combinations to the gene pool of the next generation.
(6) Changes in allelic frequencies in populations come about primarily by means of natural selection, even though random mutations occur frequently.
(7) Barriers that restrict or eliminate gene flow between the subpopulations of a species are essential for genetic and phenotypic divergence of the subpopulations of a species.
(8) Speciation is complete when gene flow does not occur between a divergent population and the population of its parent species.

monogenic (single-gene) mutations resulting in speciation are rare, it is increasingly clear that phenotypes can be altered dramatically as a result of just one or a few mutations. Indeed, there is good evidence that phenotypes can diverge rapidly by virtue of single allele differences. For example, a mutation in the *AFILA* allele in pea results in a leaf composed entirely of tendrils (fig. 0.9). Likewise, the effects of mutation on flower structure can affect pollination syndromes and thereby limit or eliminate gene flow among neighboring populations of plants. For example, flowers lacking petals (apetalous flowers) are typically wind pollinated or self-pollinated, while flowers with large numerous petals (polypetalous flowers) are generally pollinated by animals. Single-gene mutations resulting in apetalous, fertile flowers are known for mountain laurel (*Kalmia latifolia*), evening primrose (*Oenothera parodiana*), tobacco (*Nicotiana tabacum*), and a variety of annual chrysanthemum species. Conversely, monogenic mutations
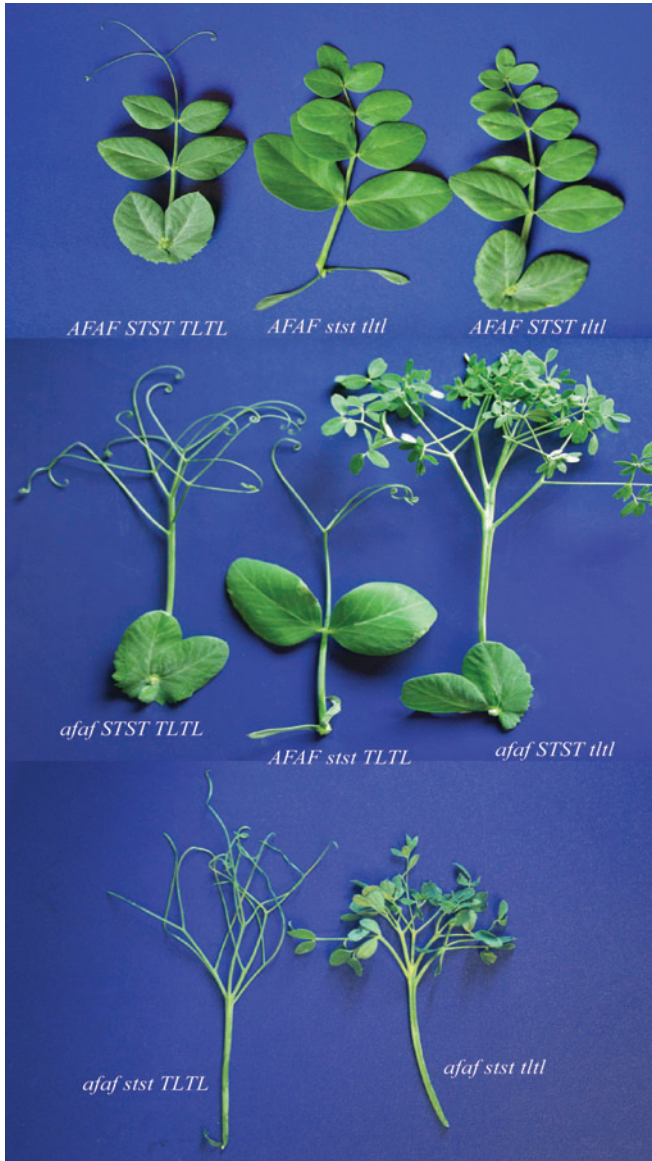
Figure 0.9. Representative leaves of eight genotypes of peas differing in their *af*, *st*, and *tl* allelic composition (see inserts for genotypic compositions). A mutation in a single gene can result in dramatic differences—for example, the wild type of pea is *AFAF STST TLTL* (shown at the upper left), whereas the *afaf STST TLTL* genotype leaf is all tendrils (shown below the wild type). Each of the three recessive allelic mutations is a naturally occurring mutation on three separate chromosomes that alter leaf architecture. In the examples shown here, each combination of alleles has been introduced into otherwise isogenic lines (i.e., all other genes in the diploid plants are homozygous). The use of isogenic lines reveals how each *af*, *st*, and *tl* allelic composition affects leaf shape.

resulting in flowers with supernumerary petals occur in mountain laurel, geranium (*Pelargonium hortorum*), soybean (*Glycine max*), gloxinia (*Sinningia speciosa*), garden nasturtium (*Tropaeolum majus*), and petunia (*Petunia* hybrids). Consider also monogenic mutations that affect floral organ identity. The mutations of the *AP3* or *PI* genes of the mouse-ear cress (*Arabidopsis thaliana*) or the *DEF* gene in snapdragon (*Antirrhinum majus*) cause petals to be replaced by sepals, and stamens to be replaced by carpels. None of these phenotypic alterations is known to have resulted in a new species. However, the structure and appearance of flowers are extremely important to attracting specific animal pollinators, and changes of the types just described can reduce or even eliminate gene flow between populations of wild-type and mutated plants that can in turn be the prelude to speciation.

Inspection of table 0.5 also reveals a serious omission in the Modern Synthesis—a failure to incorporate the insights of developmental biology when conceptualizing evolutionary mechanisms. Indeed, the Modern Synthesis was not a *synthesis* in the true meaning of the word. It did little to bring the different fields of biology together except to say "nothing in biology makes sense other than in light of evolution." Rather, it offered a reductionist approach to understanding evolution, one that abridged the mechanics of evolution to the level of population genetics. This claim may seem unwarranted. However, no less an important architect of the Modern Synthesis than Theodosius G. Dobzhansky (1900–1975) declared, "Evolution is a change in the genetic composition of populations. The study of the mechanisms of evolution falls within the province of population genetics." This perspective was grounded on a number of assumptions, some of which are extremely problematic. Four of these assumptions are particularly notable:

(1) Evolution proceeds gradually in small steps ("gradualism prevails").

(2) The mechanisms responsible for the appearance of new species are the same as those that give rise to higher taxa ("microevolution explains macroevolution").

(3) It is possible to directly map an organism's phenotype directly onto its genotype ("the genotype explains everything").

(4) Taxonomically widely separated organisms lack genetic similarities ("there are no widely shared 'old' genes").

As noted, assumptions (1) and (2) directly mirror those of Darwin—speciation is slow and thus of long duration, and the appearance of higher taxa involves the same mechanisms as those responsible for speciation. Assumptions (3) and (4) emerge directly from a single-minded focus on population genetics. Importantly, all four assumptions are incomplete at best. The monogenic mutations mentioned earlier have profound biological effects on morphology in just one generation, and we know of examples in which new plant species make their appearance over the course of a few generations, or, in the case of hybrids, one generation (see chapter 5). Likewise, epigenetic phenomena, microRNA gene silencing, and many other phenomena refute the notion that the phenotype emerges purely and simply from the genotype. It is also apparent that the co-option of "old genes" to do new things is ubiquitous in evolutionary dynamics. The mind-set of the Modern Synthesis emerged from a philosophy that failed to recognize that the developmental *arrival* of a novel phenotype is as important as the *survival* of the phenotype. This serious mistake had a number of consequences that will be explored in chapter 3.

What Is a Theory?

Before we proceed to examine evolution in the following nine chapters, it is useful to understand what is meant by "a scientific theory" such as the theory of evolution. The word "theory" has many colloquial meanings as for example "a hunch" or "an idea." However, in the sciences, the word has a much more focused and precise meaning, as for example *a predictive set of interrelated hypotheses that integrates facts to provide a broad explanation for one or more naturally occurring phenomena*. The theory of evolution is predictive (it expects adap-

tation, speciation, extinction, etc.) on the basis of a comparatively small set of hypotheses (heritable variation, natural selection, etc.) that integrates facts (empirical observations of living organisms and the fossil record) to provide a broadly applicable explanation of naturally occurring phenomena (how living things change and adapt to the world around them). Importantly, a scientific theory employs the scientific method of hypothesis building and testing, and as such it can and must be modified as new facts are brought to light. Indeed, we shall see that Darwin's theory of evolution was not complete. In fact, he got some things wrong. This is a characteristic of science because we are always learning new things and because our theories are constantly changing as new facts are learned. This is not a sign of weakness or failure. It is a sign of intellectual vigor and honesty. It is also a sign that our universe is extraordinarily complex.

Although the Darwinian theory of evolution has been modified and amplified over many decades of research, its predictive powers nevertheless remain impressive. Consider the case of Darwin's orchid, *Angraecum sesquipedale*. Early in the year 1862, the English horticulturalist James Bateman (1811–1897) sent Darwin a shipment of orchids collected in Madagascar containing an orchid bearing a beautiful star-shaped, white flower with an exceptionally long spur measuring as long as 30 cm (fig. 0.10). Inspection revealed a nectary within the tip of the spur, which prompted Darwin to hypothesize that the orchid must be pollinated by a moth with an exceptionally long proboscis (Darwin predicted a moth rather than a butterfly because the flower of *A. sesquipedale* is white rather than pigmented; see fig. B.6.1 in box 6.1 in chapter 6). On the basis of this hypothesis, which rested on the hypotheses called selection and adaptation, Darwin predicted the existence of an unknown insect (most probably a moth). In 1907, more than 20 years after his death, Darwin's hypothesis was vindicated by the discovery of a large Madagascar moth bearing a proboscis that measured on average 20 cm in length. The moth was named *Xanthopan morganii praedicta* in honor of Darwin's prediction.

Figure 0.10. Representative flowers of "Darwin's Orchid," *Angraecum sesquipedale*. On the basis of his theory of evolution and his familiarity with pollination syndromes, Darwin predicted that the white flowers of this species would be pollinated by a nocturnal moth. This prediction was vindicated more than 110 years after his death when a large Madagascar moth with a 20 cm long tongue was observed under field condition pollinating this orchid. This example typifies what a scientific *theory* means.

Nevertheless, at that time there was no direct evidence that the moth fed on the nectar of *A. sesquipedale*, or that the moth was the orchid's pollinator. The scientific method required proof. It was not until 1992, more than 110 years after Darwin's death, that *X. morganii praedicta* was *directly* observed to feed on the orchid's nectar and to transport pollen from one flower to another.

The mutualistic nature of Darwin's orchid and *X. morganii praedicta* has become a classic example of plant-insect coevolution. Perhaps more important, it epitomizes what is meant by the ability of a *scientific* theory to explain the world around us in a rational, coherent, and empirically testable way. If some one asks you, "Do you believe in evolution?" answer, "Do you believe in the sun?" We can see and measure the sun. We can see and measure evolution. The phrase *I believe* is irrelevant to the scientific method or the scientific community. The sun is a fact. Evolution is a fact as well as an idea.

> Knowledge requires us to possess both Facts and Ideas;—that every
> step in our knowledge consists in applying the ideas and the concep-
> tions furnished by our minds to the facts which observation and exper-
> iment offer us. When our conceptions are clear and distinct, when our
> facts are certain and sufficiently numerous, and when the conceptions,
> being suited to the nature of the facts, are applied to them so as to
> produce an exact and universal accordance, we attain knowledge of a
> precise and comprehensive kind, which we may term *Science*.
>
> —WILLIAM WHEWELL, *The Philosophy of the Inductive Sciences*, Part II,
> Book XI (1847)

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