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Fibonacci Numbers, the Golden Ratio, and Laws of Nature?

Mathematics required:

high school algebra, geometry, and trigonometry; concept of limits from precalculus

Mathematics introduced:

difference equations with constant coefficients and their solution; rational approximation to irrational numbers; continued fractions

1.1 Leonardo Fibonacci

Leonardo of Pisa (1175–1250), better known to later Italian mathematicians as Fibonacci (Figure 1.1), was born in Pisa, Italy, and in 1192 went to North Africa (Bugia, Algeria) to live with his father, a customs officer for the Pisan trading colony. His father arranged for the son's instruction in calculational techniques, intending for Leonardo to become a merchant. Leonardo learned the Hindu-Arabic numerals (Figure 1.2) from one of his “excellent” Arab instructors. He further broadened his mathematical horizons on business trips to Egypt, Syria, Greece, Sicily, and Provence. Fibonacci returned to Pisa in 1200 and published a book in 1202 entitled *Liber Abaci* (*Book of the Abacus*), which contains a compilation of mathematics known since the Greeks. The book begins with the first introduction to the Western business world of the decimal number system:

These are the nine figures of the Indians: 9, 8, 7, 6, 5, 4, 3, 2, 1. With these nine figures, and with the sign 0, which in Arabic is called zephirum, any number can be written, as will be demonstrated.

Since we have ten fingers and ten toes, one may think that there should be nothing more natural than to count in tens, but that was not the case in Europe at the time. Fibonacci himself was doing calculations



Figure 1.1. Statue of Fibonacci in a cemetery in Pisa. (Photograph by Chris Tung.)



Figure 1.2. The Hindu-Arabic numerals.

using the Babylonian system of base 60! (It is not as strange as it seems; the remnant of the sexagesimal system can still be found in our measures of angles and time.)

The third section of *Liber Abaci* contains a puzzle:

A certain man put a pair of rabbits in a place surrounded on all sides by a wall. How many pairs of rabbits can be produced from that pair in a year if it is supposed that each month each pair begets a new pair which from the second month on becomes productive?

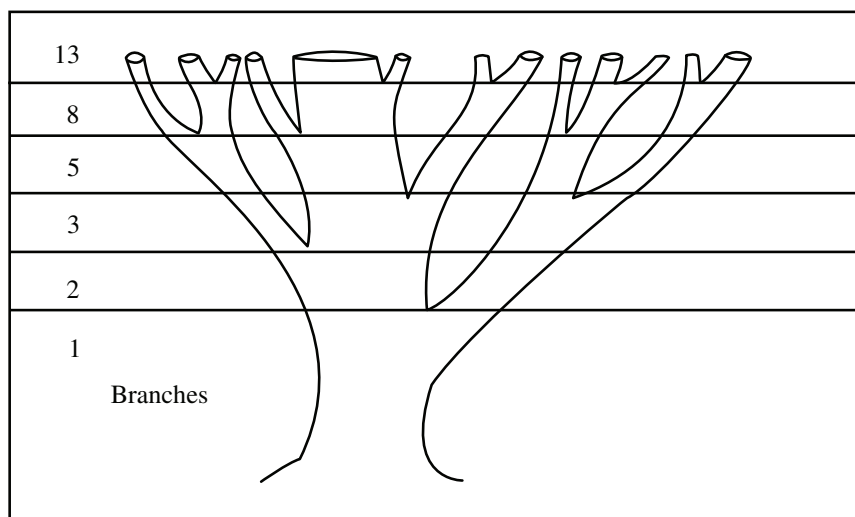


Figure 1.3. Branching of plant every month after a shoot is two months old.

In solving this problem, a sequence of numbers, 1, 1, 2, 3, 5, 8, 13, 21, 34, 55, \dots , emerges, as we will show in a moment. This sequence is now known as the Fibonacci sequence.

The above problem involving incestuous rabbits is admittedly unrealistic, but similar problems can be phrased in more plausible contexts: A plant (tree) has to grow two months before it branches, and then it branches every month. The new shoot also has to grow for two months before it branches (see Figure 1.3). The number of branches, including the original trunk, is, if one counts from the bottom in intervals of one month's growth: 1, 1, 2, 3, 5, 8, 13, \dots . The plant *Achillea ptarmica*, the "sneezewort," is observed to grow in this pattern.

The Fibonacci sequence also appears in the family tree of honey bees. The male bee, called the drone, develops from the unfertilized egg of the queen bee. Other than the queen, female bees do not reproduce. They are the worker bees. Female bees are produced when the queen mates with the drones. The queen bee develops when a female bee is fed the royal jelly, a special form of honey. So a male bee has only one parent, a mother, while a female bee, be it the queen or a worker bee, has both a mother and a father. If we count the number of parents and grandparents and great grandparents, etc., of a male bee, we will get 1, 1, 2, 3, 5, 8, \dots , a Fibonacci sequence.

Let's return to the original mathematical problem posed by Fibonacci, which we haven't yet quite solved. We actually want to solve it more generally, to find the number of pairs of rabbits n months after the first pair was introduced. Let this quantity be denoted by F_n .

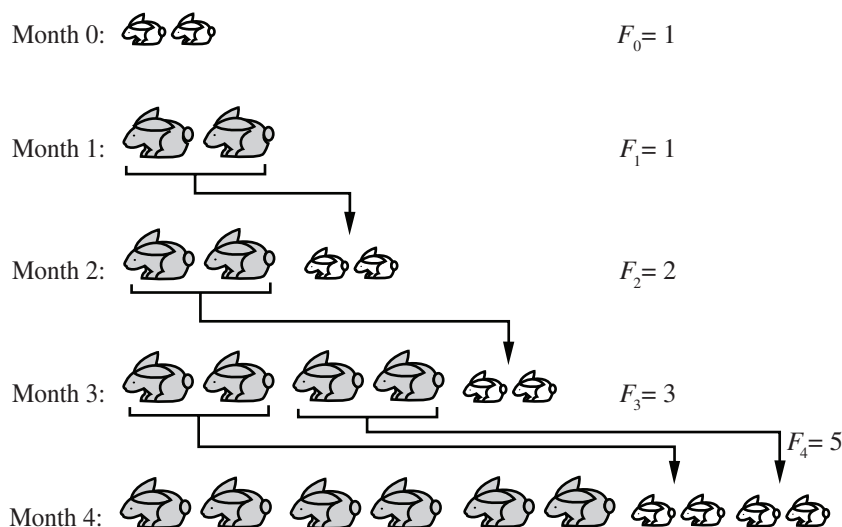


Figure 1.4. Rabbits in the Fibonacci puzzle. The small rabbits are nonproductive; the large rabbits are productive.

We assume that the initial pair of rabbits is one month old and that we count rabbits just before newborns arrive.

One way to proceed is simply to *enumerate*, thus generating a sequence of numbers. Once we have a sufficiently long sequence, we would hopefully be able to see the now famous Fibonacci pattern (Figure 1.4).

After one month, the first pair becomes two months old and is ready to reproduce, but the census is taken before the birth. So $F_1 = 1$, but $F_2 = 2$; by the time they are counted, the newborns are already one month old. The parents are ready to give birth again, but the one-month-old offspring are too young to reproduce. Thus $F_3 = 3$. At the end of three months, both the original pair and its offspring are productive, although the births are counted in the next period. Thus $F_4 = 5$. A month later, an additional pair becomes productive. The three productive pairs add three new pairs of offspring to the population. Thus $F_5 = 8$. At five months, there are five productive pairs: the first-generation parents, four second-generation adults, and one third-generation pair born in the second month. Thus $F_6 = 13$. It now gets more difficult to keep track of all the rabbits, but one can use the aid of a table to keep account of the ages of the offspring. With some difficulty, we obtain the following sequence for the number of rabbit pairs after n months, for $n = 0, 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, \dots$: 1, 1, 2, 3, 5, 8, 13, 21, 34, 55, 89, 144, 233, 377, \dots

This is the sequence first generated by Fibonacci. The answer to his original question is $F_{12} = 233$.

If we had decided to count rabbits after the newborns arrive instead of before, we would have to deal with three types of rabbits: newborns, one-month-olds, and mature (two-month-old or older) rabbits. In this case, the Fibonacci sequence would have shifted by one, to: 1, 2, 3, 5, 8, 13, 21, 34, 55, 89, 144, 233, ... The initial 1 is missing, which, however, can be added back if we assume that the first pair introduced is newborn. It then takes two months for them to become productive. The discussion below works with either convention.

To find F_n for a general positive integer n , we hope that we can see a pattern in the sequence of numbers already found. A sharp eye can now detect that any number in the sequence is always the sum of the two numbers preceding it. That is,

$$F_{n+2} = F_{n+1} + F_n, \quad \text{for } n = 0, 1, 2, 3, \dots \quad (1.1)$$

A second way of arriving at the same recurrence relationship is more preferable, because it does not depend on our ability to detect a pattern from a partial list of answers:

Let $F_n(k)$ be the number of k -month-old rabbit pairs at time n . These will become $(k + 1)$ -month-olds at time $n + 1$. So,

$$F_{n+1}(k + 1) = F_n(k).$$

The total number of pairs at time $n + 2$ is equal to the number at $n + 1$ plus the newborn pairs at $n + 2$:

$$F_{n+2} = F_{n+1} + \text{new births at time } n + 2.$$

The number of new births at $n + 2$ is equal to the number of pairs that are at least one month old at $n + 1$, and so:

$$\begin{aligned} \text{New births at } n + 2 &= F_{n+1}(1) + F_{n+1}(2) + F_{n+1}(3) + F_{n+1}(4) + \dots \\ &= F_n(0) + F_n(1) + F_n(2) + F_n(3) + \dots \\ &= F_n. \end{aligned}$$

Therefore,

$$F_{n+2} = F_{n+1} + F_n,$$

which is the same as Eq. (1.1). This recurrence equation is also called the renewal equation. It uses present and past information to predict the future. Mathematically it is a second-order difference equation.

To solve Eq. (1.1), we try, as we generally do for linear difference equations whose coefficients do not depend on n ,

$$F_n = \lambda^n,$$

for some as yet undetermined constant λ . When we substitute the trial solution into Eq. (1.1), we get

$$\lambda^{n+2} = \lambda^{n+1} + \lambda^n.$$

Canceling out λ^n , we obtain a quadratic equation,

$$\lambda^2 = \lambda + 1, \quad (1.2)$$

which has two roots (solutions):

$$\lambda_1 = \frac{1}{2}(1 + \sqrt{5}) \text{ and } \lambda_2 = \frac{1}{2}(1 - \sqrt{5}) = -\frac{1}{\lambda_1}.$$

Thus λ_1^n is a solution, and so is λ_2^n . By the principle of linear superposition, the general solution is

$$F_n = a\lambda_1^n + b\lambda_2^n, \quad (1.3)$$

where a and b are arbitrary constants. If you have doubts on the validity of the superposition principle used, I encourage you to plug this general solution back into Eq. (1.1) and see that it satisfies that equation no matter what values of a and b you use. Of course these constants need to be determined by the initial conditions. We need two such auxiliary conditions since we have two unknown constants. They are $F_0 = 1$ and $F_1 = 1$. The first requires that $a + b = 1$, and the second implies that $\lambda_1 a + \lambda_2 b = 1$. Together, they uniquely determine the two constants. Finally, we find:

$$F_n = \frac{1}{\sqrt{5}} \left(\frac{1 + \sqrt{5}}{2} \right)^{n+1} - \frac{1}{\sqrt{5}} \left(\frac{1 - \sqrt{5}}{2} \right)^{n+1}, \quad n = 0, 1, 2, 3, \dots$$

(1.4)

With the irrational number $\sqrt{5}$ in the expression, it is surprising that Eq. (1.4) would always yield whole numbers, 1, 1, 2, 3, 5, 8, 13, \dots , when n goes from 0, 1, 2, 3, 4, 5, \dots , but you can verify that amazingly it does.

1.2 The Golden Ratio

The number $\lambda_1 = \frac{1}{2}(1 + \sqrt{5})$ is known as the *Golden Ratio*. It has also been called the *Golden Section* (in an 1835 book by Martin Ohm) and, since the 16th century, the *Divine Proportion*. It is thought to reflect the ideal proportions of nature and to even possess some mystical powers. It is an irrational number, now denoted by the Greek symbol Φ :

$$\Phi = 1.6180339887 \dots$$

It does have some very special, though not so mysterious, properties. For example, its square,

$$\Phi^2 = 2.6180339887 \dots,$$

is obtainable by adding 1 to Φ . Its reciprocal,

$$1/\Phi = 0.6180339887 \dots,$$

is the same as subtracting 1 from Φ . These properties are not mysterious at all, if we recall that Φ is a solution of Eq. (1.2).

In terms of Φ , the general solution (1.3) can be written as

$$F_n = a\Phi^n + b\left(-\frac{1}{\Phi}\right)^n.$$

Since $\Phi > 1$, the second term diminishes in importance as n increases, so that for $n \gg 1$,

$$F_n \approx a\Phi^n.$$

Therefore the ratio of successive terms in the Fibonacci sequence approaches the Golden Ratio:

$$\boxed{\frac{F_{n+1}}{F_n} \rightarrow \frac{a\Phi^{n+1}}{a\Phi^n} = \Phi = 1.6180339887 \dots, \text{ as } n \rightarrow \infty.} \quad (1.5)$$

(In fact, since this property about the ratio converging to the Golden Ratio is independent of a and b , as long as a is not zero, it is satisfied by all solutions to the difference equation (1.1), including the Lucas sequence, which is the sequence of numbers starting with $F_0 = 2$ and $F_1 = 1$: 2, 1, 3, 4, 7, 11, 18, 29, ...).

For our later use, we also list the result

$$\boxed{\frac{F_{n+2}}{F_n} \rightarrow \frac{a\Phi^{n+2}}{a\Phi^n} = \Phi^2.} \quad (1.6)$$

As you may recall, an irrational number is a number that cannot be expressed as the ratio m/n of two integers, m and n . Mathematicians sometimes are interested in the *rational approximation* of an irrational number; that is, finding two integers, m and n , whose ratio, m/n , gives a good approximation of the irrational number with an error that is as small as possible under some constraints. For example, the irrational number $\pi = 3.14159265\dots$ can be approximated by the ratio $22/7 = 3.142857\dots$, with error 0.00126. This is the best rational approximation if n is to be less than 10. When we make m and n larger, the error goes down rapidly. For example, $355/113$ is a rational approximation of π (with n less than 200) with an error of 0.000000266. We measure the degree of irrationality of an irrational number by how slowly the error of its best rational approximation approaches zero when we allow m and n to get bigger and bigger. In this sense π is “not too irrational.”

From Eq. (1.5) we see that the value of Φ can thus be approximated by the rational ratio: $8/5 = 1.6$, or $13/8 = 1.625$, or $21/13 = 1.615385\dots$, or $34/21 = 1.619048\dots$, or $55/34 = 1.617647\dots$, or $89/55 = 1.618182\dots$, or $144/89 = 1.617978\dots$. The ratios of successive terms in the Fibonacci sequence will eventually converge to the Golden Ratio. One therefore can use the ratio of successive Fibonacci numbers as the rational approximation to the Golden Ratio. Such rational ratios, however, converge to the Golden Ratio extremely slowly. Thus we might say that the Golden Ratio is the *most irrational* of the irrational numbers. (How do we know it is the most irrational of the irrational numbers? A proof requires the use of continued fractions. See exercise 2 for some examples.)

More importantly, the Golden Ratio has its own geometrical significance, first recognized by the Greek mathematicians Pythagoras (560–480 BC), and Euclid (365–325 BC). The Golden Ratio is the only positive number that, when 1 is subtracted from it, equals its reciprocal. Euclid in fact defined it, without using the name Golden Ratio, when he studied the division of a line into what he called the “extreme and mean ratio”:

A straight line is said to have been cut in extreme and mean ratio when, as the whole line is to the greater segment, so is the greater to the lesser.

1.2 The Golden Ratio

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Figure 1.5. A straight line cut into extreme and mean ratios.

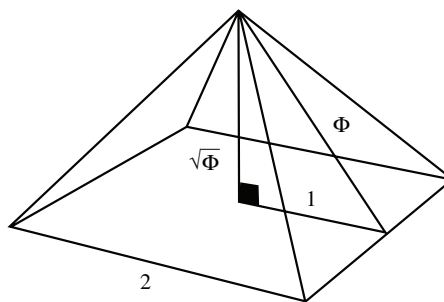


Figure 1.6. The Great Pyramid at Giza and the “Egyptian Triangle.”

(Does this sound like Greek to you? If so, you may find Figure 1.5 helpful. Consider the straight line abc , cut into two segments ab and bc , in such a way that the “extreme ratio” $\overline{abc}/\overline{ab}$ is equal to its “mean ratio” $\overline{ab}/\overline{bc}$. Without loss of generality, let the length of small segment \overline{bc} be 1, and \overline{ab} be x , so the whole line \overline{abc} is $1 + x$. The line is said to be cut in extreme and mean ratio when $(1 + x)/x = x/1$; this is the same as $x^2 = x + 1$, which is Eq. (1.2). Φ is the only positive root of that equation.)

Many authors reported that the ancient Egyptians possessed the knowledge of the Golden Ratio even earlier and incorporated it in the geometry of the Great Pyramid of Khufu at Giza, which dates to 2480 BC. Midhat Gazale, who was the president of AT&T-France, wrote in his popular 1999 book, *Gnomon: From Pharaohs to Fractals*:

It was reported that the Greek historian Herodotus learned from the Egyptian priests that the square of the Great Pyramid’s height is equal to the area of its triangular lateral side.

Referring to Figure 1.6, we consider the upright right triangle formed by the height of the pyramid (from its base to its apex), the slanted height of the triangle on its lateral side (the length from the base to the apex of the pyramid along the slanted lateral triangle), and a horizontal line joining these two lines inside the base. We see that if the above statement is true, then the ratio of the hypotenuse to the base of that triangle is equal to the Golden Ratio. (Show this!) However, as pointed out by Mario Livio in his wonderful 2002 book, *The Golden Ratio*, Gazale was repeating an earlier misinterpretation by the English

author John Taylor in his 1859 book, *The Great Pyramid: Why Was It Built and Who Built It*, in which Taylor was trying to argue that the construction of the Great Pyramid was through divine intervention. What the Greek historian Herodotus (ca. 485–425 BC) actually said was: “Its base is square, each side is eight plethra long and its height the same.” One plethron was 100 Greek feet, approximately 101 English feet (see Fischler, 1979; Markowsky, 1992).

Nevertheless, there is no denying that the physical dimensions of the Great Pyramid as it stands now do give a ratio of hypotenuse to base rather close to the Golden Ratio. The base of the pyramid is approximately a square with sides measuring 756 feet each, and its height is 481 feet. So the base of the upright right triangle is $756/2 = 378$ feet, while the hypotenuse is, by the Pythagorean Theorem, 612 feet. Their ratio is then $612/378 = 1.62$, which is in fact quite close to the Golden Ratio. The debate continues. All we can say is that, casting aside the claims of some religious cults, there is no historical or archeological evidence that the ancient Egyptians knew about the Golden Ratio.

1.3 The Golden Rectangle and Self-Similarity

An application of Euclid’s subdivision of a line is to construct a rectangle with the proportion $1 : \Phi$ as the ratio of its short to long side. This rectangle is called the *Golden Rectangle*. Since some of the more familiar proportions in human anatomy, such as the width to the height of an adult face, or the length measured from the top of the head to the navel and from the navel to the bottom of the feet, are *roughly* in the ratio of $1 : \Phi$, speculations abound that artists and sculptors through the ages consciously incorporated the Golden Ratio in their work (see Figure 1.7). (See a critical discussion in Markowsky [1992].)

We shall not be concerned with the subject of the Golden Ratio in art and in defining beauty here. Instead we wish to briefly point out another interesting property of the Golden Rectangle. A Golden Rectangle can be subdivided into a square and a smaller rectangle with the ratio of its short to long side equaling $1/\Phi : 1 = 1 : \Phi$ (since $\Phi - 1 = 1/\Phi$). This is another Golden Rectangle! (See Figure 1.8.) The latter can be subdivided, ad infinitum, into even smaller but similar shapes. The resulting entity is *self-similar*. That is, if you zoom in on a smaller rectangle—with even smaller rectangles and squares embedded in it—and magnify it, it will look the same as the original, bigger rectangle. The property that an object will look the same at all scales is called *self-similarity*. This property is fundamental to the modern concept of *fractals*. (See the exercises for some discussion on fractals.)

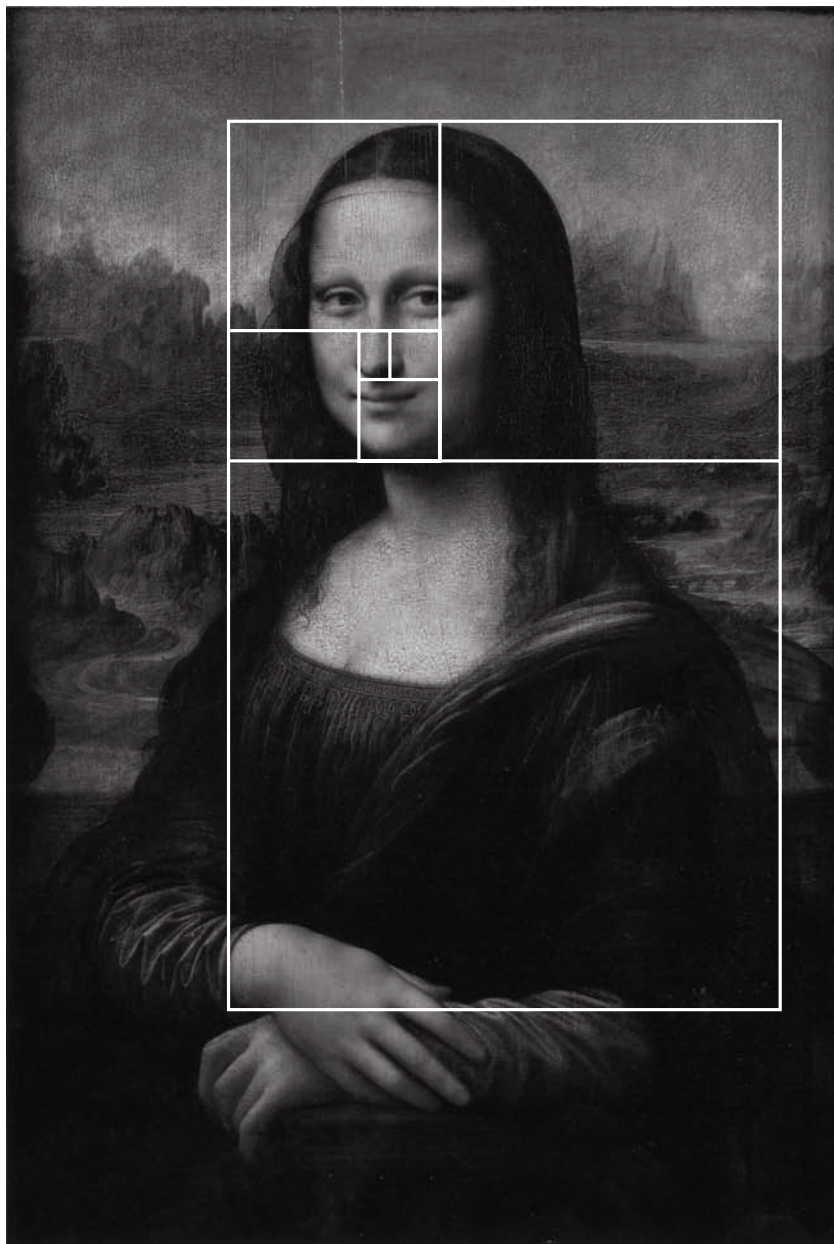


Figure 1.7. Leonardo da Vinci's *Mona Lisa*.

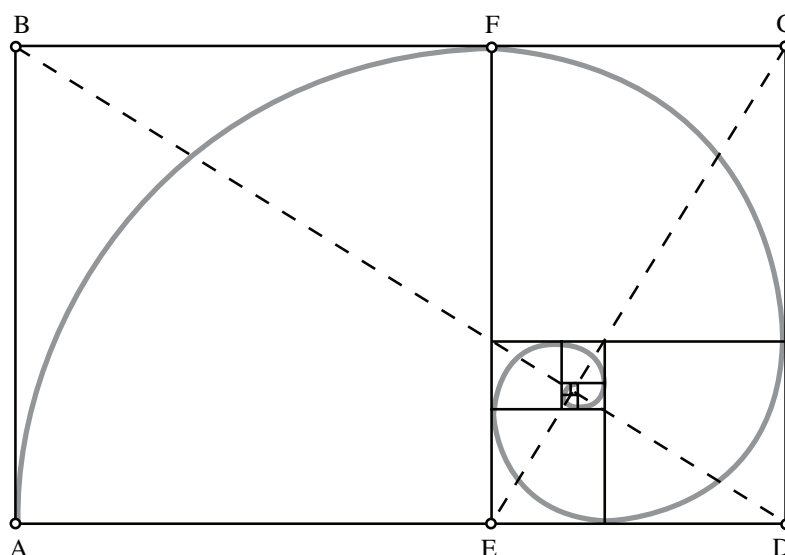


Figure 1.8. Golden Rectangles $AE = AB = 1$, $AD = \Phi$, $FC = \Phi - 1 = 1/\Phi$.

If we join the two opposite corners of each square using a quarter circular arc and connect these arcs together (Figure 1.8), we will obtain a pseudospiral, winding in the limit to a point, which is fancifully called “the eye of God.” (The pseudospiral approximates very well a true *logarithmic spiral*, which is also called the *equiangular spiral*. At every point on the logarithmic spiral the angle the tangent makes with the line drawn to the center is always the same.) The logarithmic spiral is self-similar, because it looks the same whatever the magnification. This self-similar property of the spiral may be the reason why some seashells are also in the shape of a logarithmic spiral (Figure 1.9), so as to accommodate the growing body of the mollusk. As it grows, the mollusk constructs larger and larger chambers (and seals off the smaller chambers it no longer uses). Each new chamber has the same familiar shape as the old one the mollusk evacuates.

1.4 Phyllotaxis

Phyllotaxis is the study of leaf arrangements in plants. Fibonacci numbers are found to be “prevalent” in the phyllotaxis of various trees, in seed heads, pinecones, and sunflowers. It is still an ongoing effort by botanists and applied mathematicians to try to understand why this is so from biological and mechanical perspectives.

As the stem of a plant grows upward, leaves sprout to its side, with new leaves above the old ones. How are the new and old leaves

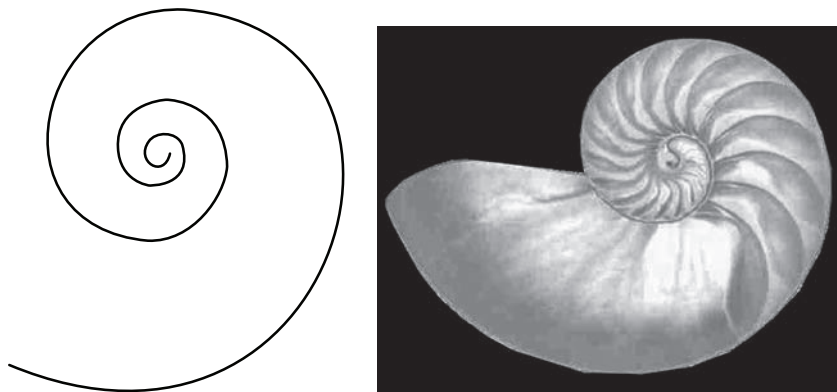


Figure 1.9. The spiral of the Nautilus shell. (Photo courtesy of Bill Strange.)

arranged? Is there a pattern? Theophrastus (372–287 BC) appears to have been the first to notice, in his writing *Enquiries into Plants*, that there is indeed a pattern: “Those that have flat leaves have them in a regular series.” The painter Leonardo da Vinci (1452–1519) and the astronomer Johannes Kepler (1571–1630) also wrote on the subject. Kepler in particular noted the connection between the Fibonacci numbers and leaf arrangements. In 1837, the Bravais brothers (Auguste, a crystallographer, and Louis, a botanist) discovered that a new leaf generally advances by the same angle from the previous leaf, and that angle is usually close to 137.5° . That is, if you look down from above on the plant and measure the angle formed between a line drawn from the stem to the leaf and a corresponding line for the next leaf, you will find that there is generally a fixed angle, called the *divergence angle*. You may think that the divergence angle should be something simple, such as 180° , so that the new leaf will be on the opposite side of the stem from the older leaf, “to provide balance” for the plant. This turns out *not* to be advantageous for the plant if it has many leaves, assuming that the sun and rain come from above (vertically). This is because if leaf 0 and leaf 1 are arranged this way, leaf 2 will then be directly above leaf 0, blocking its exposure to sun and moisture.

Generalizing this argument, we note that any divergence angle that is an integer fraction of a circle, i.e., equal to $360^\circ/m$, with m being an integer, is also not optimal for the plant. This is because such an arrangement of leaves is periodic; eventually some new leaves will be directly above some older ones, and the pattern repeats for newer leaves. For example, for $m = 3$, the fourth leaf will be directly above the first. (Similarly, a divergence angle of $360^\circ n/m$ will also not be optimal because it is again periodic.) It would appear that the most optimal

arrangement would be obtained if we replaced the integer m by an *irrational number*—the more irrational the better. And the best number would seem to be $\Phi = 1.618 \dots$, the Golden Ratio, the most irrational of all irrational numbers. And so, naturally, the *divergence angle* $= 360^\circ / \Phi = 222.5^\circ$, which is the same as $360 - 222.5 = 137.5^\circ$, measuring from the other direction, would appear to be the optimal angle. The divergence angle of 137.5° is called the Golden Angle.

Botanists define the *phyllotactic ratio* as the fraction of a circle through which a new leaf turns from the previous (older) leaf. So in this case the phyllotactic ratio is $1/\Phi = 0.618 \dots$. Since this is more than half of a circle, one may want to measure the angle from the other direction (e.g., counterclockwise instead of clockwise). In that case the phyllotactic ratio would be $1 - 1/\Phi = 1/\Phi^2 = 0.382 \dots$. Given the propensity of botanists to list phyllotactic ratios as ratios of integers, it is not surprising that ratios of every other Fibonacci number show up in rational approximation to the phyllotactic ratio of $1/\Phi^2$, in the form of Eq. (1.6). That is,

$$\text{Phyllotactic ratio} = \frac{1}{\Phi^2} \approx \frac{F_n}{F_{n+2}}, \quad (1.7)$$

where F_n is one of the Fibonacci numbers. The phyllotactic ratio is the ratio of *every other* Fibonacci number. If one measures the angle in the other direction, e.g., clockwise rather than counterclockwise, one will detect a different set of Fibonacci numbers:

$$\text{Phyllotactic ratio} = \frac{1}{\Phi} \approx \frac{F_n}{F_{n+1}}, \quad (1.8)$$

according to Eq. (1.5). This may explain why *three consecutive members* of the Fibonacci sequence are often found in the phyllotactic ratios of a single plant, a situation that may appear mysterious at first sight.

The above argument applies to plants with many, many leaves (in fact, an infinite number of leaves) and under the assumption that the maximum exposure to the sun is the only determining factor for the arrangement of leaves in a plant. Neither of these assumptions is realistic. It remains unexplained why the prevalent tendency is for realistic plants to have a divergence angle close to 137.5° . Nevertheless, if a plant must choose a *fixed* divergence angle, *why not* choose 137.5° ? There is no *better* angle from which to choose. Now *suppose* a plant of finite height (and with a finite number of leaves) grows leaves at this fixed angle. Then what phyllotactic ratio would be observed? It would, of course, be Eq. (1.7) or (1.8), depending on the direction from which

you measure the angle. A plant with a larger number of leaves would generally have a larger value of n , giving a better rational approximation to the Golden Ratio than plants with fewer leaves.

Some examples of phyllotactic ratios for selected plants are given below. A ratio of, e.g., $3/8$ means that in three turns of a circle one would find leaf 8 almost directly above leaf 0.

Apple, apricot, cherry, coast live oak, holly, plum	$2/5$
Pear, weeping willow, poplar	$3/8$
Pussy willow, almond	$5/13$

The above explanation of the phyllotactic ratio is somewhat unsatisfactory because we have not explained why the divergence angle is prevalently 137.5° . Surely the preference for maximum exposure to the overhead sun need not be absolute. There must be some other constraints that we have not included in our arguments so far.

A better, though still controversial, argument goes a little deeper in the developmental biology of plants, as we will consider in the next section.

1.5 Pinecones, Sunflowers, and Other Seed Heads

Smith College Botanical Gardens maintains a very informative website on phyllotaxis (<http://www.maven.smith.edu/~phylo/>). Recently, two Smith College mathematics professors, Pau Atela and Christophe Golé, along with a colleague, Scott Hotton from Miami University, developed a mathematical model (Atela, Golé, and Hotton, 2002) that can explain the prevalence of a particular divergence angle and the Fibonacci phyllotaxis in seed heads.

A pinecone can be viewed as a “plant” with a very short stem on which many “leaves” (scales) grow, with the newer scales developing near the tip (Figure 1.10). Sunflower heads and other seed heads (Figure 1.11) are extreme versions of such a “plant,” where the arrangement becomes two dimensional. The new “leaves” (florets) sprout near the center, and as they grow older and bigger they are displaced radially outward. New florets do not grow on top of the old, because then the old florets would be completely blocked from the sun. Perhaps in these cases, optimizing exposure to the sun may take on more importance than in plants with long stems whose leaves are separated by finite vertical distances. In such tightly packed plants, however, another factor needs to be taken into account, that of the efficiency of packing as the florets or seeds grow.

Let’s first state what we would like to explain. First is the divergence angle, of course: How does a plant know to pick 137.5° ? Second is

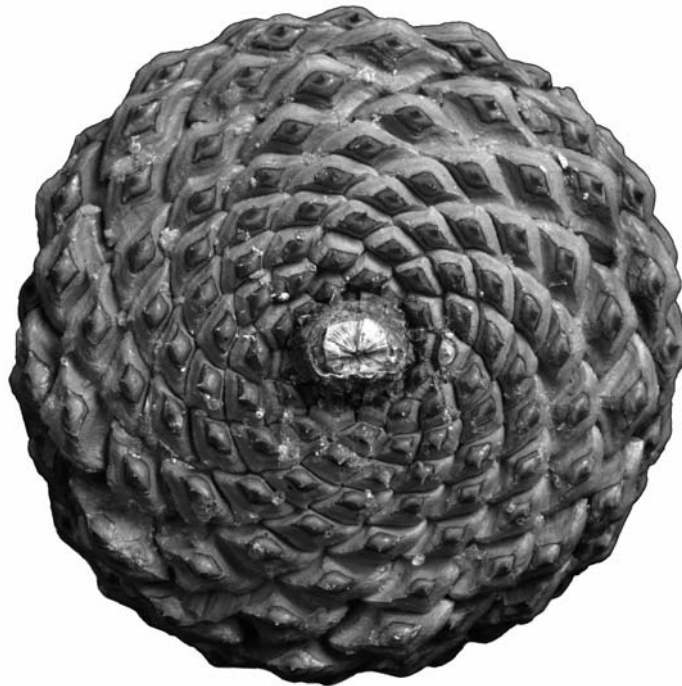


Figure 1.10. A pinecone viewed from the top. In this view, your eyes will pick up 8 counterclockwise spirals and 13 clockwise spirals. (Photo by Rolf Rutishauser, University of Zurich, Switzerland, and used by permission; also courtesy of Atela & Golé, <http://math.smith.edu/phyllo>.)

a phenomenon that is more apparent in tightly packed seed heads than in leaf arrangements on a branch, and that is the appearance of clockwise and counterclockwise spirals, whose numbers follow the Fibonacci sequence. In Figure 1.10 we show a pinecone. Looking at the pinecone from the top, your eye will pick up spirals. There are actually two sets of spirals in this picture: 8 counterclockwise and 13 clockwise. These spirals are called *parastichies*, and we say that this pinecone has a *parastichy number* of (8, 13). These, mysteriously, are two consecutive numbers in the Fibonacci sequence. Even larger parastichy numbers can be found in sunflower heads. Most common are (34, 55), but larger sunflowers with parastichy numbers of (55, 89), (89, 144), and even (144, 233) have been seen. In a way these are artificial patterns that our eyes pick up; an individual scale (or floret) does not move along such a spiral as it grows away from the center of the stem. It is just that our eyes tend to connect the scales closest to each other

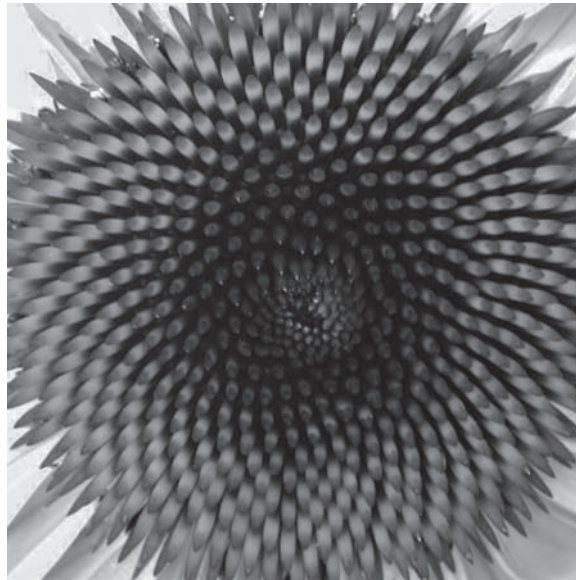


Figure 1.11. The seed head of the coneflower, a member of the daisy family. Note the apparent clockwise and counterclockwise spirals picked up by your eyes. (Photo by Tim Stone and used by permission.)

to form a pattern, and the same scale can be a member of both a counterclockwise spiral and a clockwise spiral. That our eyes will pick up these counter-rotating spirals in consecutive Fibonacci numbers in closely packed points separated by 137.5° was shown in 1907 by the German mathematician G. van Iterson. It is easier for you to show this by *simulation*, i.e., to plot these points on a sheet of paper or generate them on a computer monitor, than it is for us to prove it mathematically. This simulation is done in Figure 1.12, where the florets numbered higher are older.

1.6 The Hofmeister Rule

The patterns we see in large sunflower seed heads are actually already present when the sunflower's blossom is only 2 mm in diameter. In other plants, an electron microscope is needed to see these patterns present in their small shoot tips, called *meristems* (Figure 1.13). A meristem is the growing tip of a plant, which is usually dome shaped. Around the apex of a meristem, cells develop that will later grow to

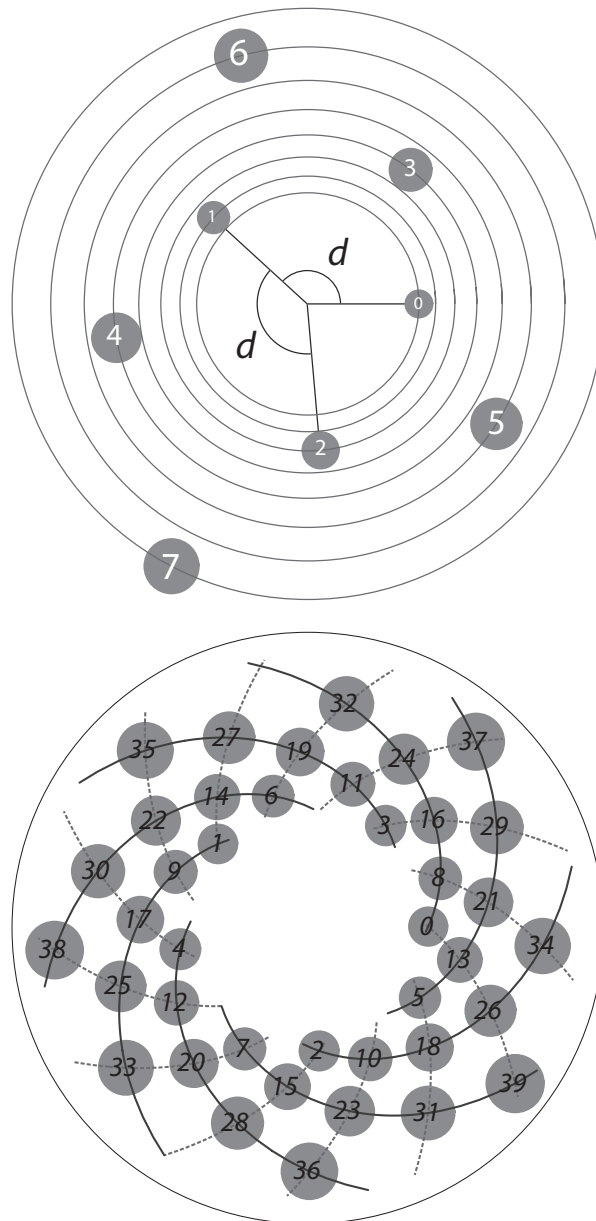


Figure 1.12. In this simulation, points are placed successively at a divergence angle of $d = 137.5^\circ$, then moved radially as they grow larger. When they are packed close together, our eyes pick up counter-rotating spirals: 8 counterclockwise and 13 clockwise in the example shown in the bottom panel. (Courtesy of Atela & Golé, <http://math.smith.edu/phylo/>.)

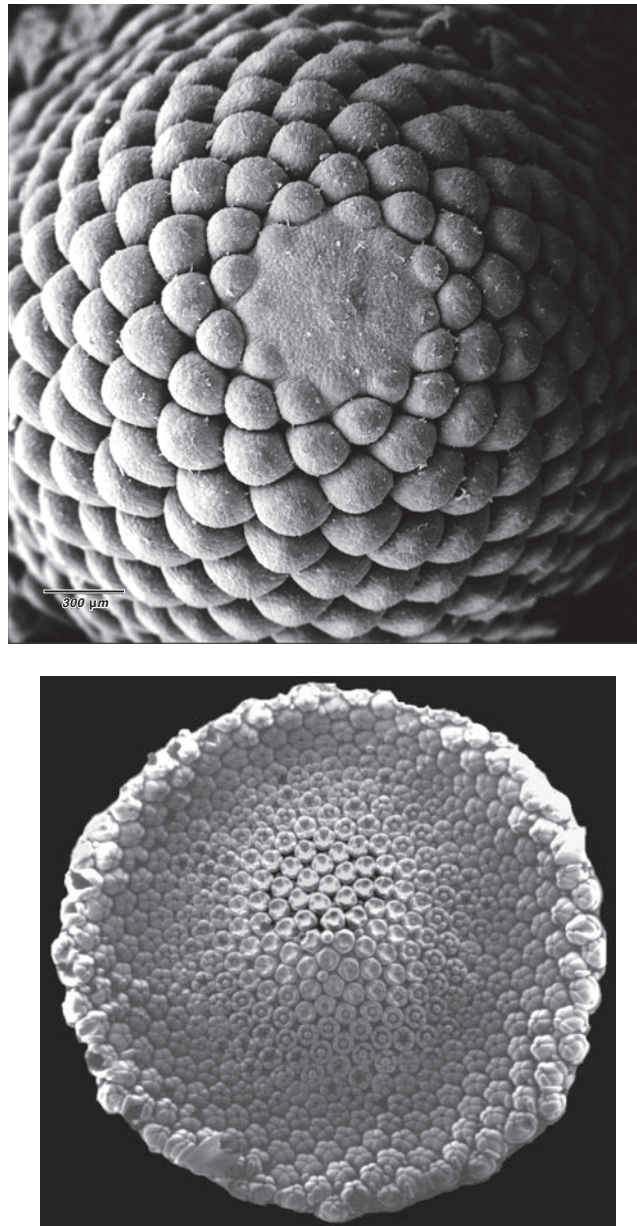


Figure 1.13. The meristem of Norway Spruce (top) has spiral parastichy (8, 13). These are primordia of needles. The meristem of artichoke (bottom) has spiral parastichy (34, 55). The primordia are future hairs in the artichoke heart. (Photo of Norway spruce by Rolf Rutishauser, University of Zurich, Switzerland, and used by permission; photo of artichoke courtesy of Jacques Dumais, <http://math.smith.edu/phyllo>.)

become leaves, petals, or florets. These “embryonic leaves” are called *primordia*. At the stage of their generation, the primordial bulges are crowded together. In 1868, from his microscopic study of plant meristems, the botanist Wilhem Hofmeister proposed that a new primordium always forms in the least crowded spot along the meristem ring. This is now known as the Hofmeister rule. The location of that least crowded spot will depend on how fast the older primordia move away from the apex as they grow. It is not yet agreed how they know to move away “to make room” for new primordia.

1.7 A Dynamical Model

In the mathematical model of Atela, Golé, and Hotton (2002), the essential features of primordial placement and growth are represented by the set of divergence angles $\{d_1, d_2, d_3, \dots\}$ and the magnification factors on the successive distance of the primordium from the center of the apex, $G > 1$, as it grows away from the apex. (Refer to Figure 1.12, but allow the angles d to be different and arbitrary.)

In a *dynamical* model, a primordium first forms at one point along the edge of the circular apex and then moves radially away from the center as the shoot grows. According to Hofmeister’s rule, the next primordium is to be placed farthest away from the first one along the apex ring. It is thus placed 180° away from it, on the other side of the circle. The placement of the third primordium will depend on how fast the first point is moving away from the edge of the apex. In the extreme case, if the first point moves away from the apex very rapidly, the third point should be placed close to where the first point was originally placed, because that is where the third point is farthest away from the second point; the location of the first point is by now too far away to matter. In this case, the divergence angle for the third point is 180° . In this extreme case, the primordia would occupy two radial lines, with a divergence angle of 180° . This yields a parastichy number $(1, 1)$. Something interesting happens when we reduce the growth rate from this extreme value. Then the original position of the first point is no longer necessarily the least crowded spot for the placement of the third point, because now the first point is in the way. The third point should be placed around the apex ring at a location that minimizes its distance from both the first and the second points. This then determines its divergence angle to be somewhere between 180° and 90° . The process is continued for the placement of the fourth point along the apex ring, which has to minimize its distance from all the preceding points. The resulting divergence angle fluctuates a little as more and more

points are placed and soon settles down to a *fixed* angle, i.e., $d_1 = d_2 = d_3 = \dots = d$. As G gets smaller (but still $G > 1$), the divergence angle approaches the Golden Angle: $d = 137.5^\circ$. At the same time as the divergence angle is getting closer to the Golden Angle, the parastichy number first becomes (1, 2) or (2, 1), depending on the direction of the spiral one is following. The branch (1, 2) then becomes (3, 2), then (3, 5), \dots , (F_n, F_{n+1}) , as G is slowly reduced, where F_n belongs to the Fibonacci sequence.

The authors point out that when plants make the transition from a vegetative state to a flowering state, the rate at which the primordia are growing apart decreases, and that is when Fibonacci-like parastichy is observed. It therefore appears that the observed appearance of Fibonacci numbers and the Golden Angle may be dictated by the need of the meristem to pack primordia efficiently when they are crowded together.

Recently, a well-known applied mathematician, Professor Alan Newell, and his graduate student Patrick Shipman at the University of Arizona proposed a different model to explain the appearance of Fibonacci numbers in the counter-rotating spirals on plants such as the cactus. Starting with the observation that the spiral patterns are already built into the plant at its earliest developmental stage, and further observing that the tender tip of a growing plant is capped by a thin outer shell, they propose that the spiral pattern is formed as the shell buckles into spiral ridges, so as to relieve mechanical stress. Their mathematical model and analysis appear in the April 23, 2004, issue of *Physical Review Letters*.

1.8 Concluding Remarks

When we observe nature, we often find certain patterns repeating themselves across a wide range of phenomena. Do these patterns reflect the laws of nature? Science would give more credence to those patterns that can be explained by some physically or biologically based mechanisms. A way to test these mechanisms is to incorporate the hypotheses into a mathematical model and then see if the model's predictions agree with observations. It appears that many of the reported sightings of the Golden Ratio in nature may be the result of chance: There are billions and billions of plants and some of them even by random chance would give the appearance of Fibonacci parastichy. However, given a prevalent tendency for plants to follow such a pattern, it is a fruitful area for botanists and mathematicians to build models for the purpose of seeking answers to the question, "Why?"

1.9 Exercises

1. A puzzle on inheritance

Fibonacci has this puzzle in *Liber Abaci*: A man whose end was approaching summoned his sons and said, “Divide my money as I shall prescribe.” To his eldest son, he said, “You are to have 1 bezant and a seventh of what is left.” To his second son, he said, “Take 2 bezants and a seventh of what remains.” To the third son, he said, “You are to take 3 bezants and a seventh of what is left.” Thus he gave each son 1 bezant more than the previous son and a seventh of what remained, and to the last son all that was left. After following their father’s instructions with care, the sons found that they had shared their inheritance equally. How many sons were there, and how large was the estate? Solve this puzzle.

2. Continued fractions

- a. Show that the Golden Ratio can be expressed in the form of a continued fraction:

$$\Phi = 1 + \frac{1}{1 + \frac{1}{1 + \frac{1}{1 + \frac{1}{1 + \dots}}}}$$

Hint: Start with the equation that the Golden Ratio satisfies: $x^2 = x + 1$. Divide by x to get $x = 1 + 1/x$. Substitute $x = 1 + 1/x$ for the x in the denominator, and repeat the process.

- b. Show that $\sqrt{2}$ can be written in a continued fraction of the form

$$\sqrt{2} = 1 + \frac{1}{2 + \frac{1}{2 + \frac{1}{2 + \dots}}}$$

Hint: Write $\sqrt{2} = 1 + 1/x$ and show that x satisfies $x^2 = 2x + 1$. Divide by x to get $x = 2 + 1/x$. Substitute $x = 2 + 1/x$ for the x in the denominator, and repeat the process.

- c. You don't need to do anything for this part. The irrational number $e = 2.71828$ is defined by the limit

$$e = \lim_{n \rightarrow \infty} (1 + 1/n)^n.$$

Euler showed that it can be written in the following continued fraction:

$$e = 2 + \frac{1}{1 + \frac{1}{2 + \frac{2}{3 + \frac{3}{4 + \frac{4}{5 + \frac{5}{6 + \dots}}}}}}$$

The irrational number π can be written in a continued fraction as (discovered by Brouncker):

$$\pi = 3 + \frac{1^2}{6 + \frac{3^2}{6 + \frac{5^2}{6 + \frac{7^2}{6 + \dots}}}}$$

- d. Truncate each of the continued fractions in (a), (b), and (c) at successive levels to obtain a rational approximation and compare the resulting approximation with the value of the original irrational number. Note and compare the convergence rates of the successive approximations for each irrational number in (a), (b), and (c).

3. The Hardy-Weinberg law in genetics

This law concerns the genetic make-up of a population from one generation to the next. It states that in sexually reproducing organisms, in the absence of genetic mutation, factors (called *alleles*) determining inherited traits are passed down unchanged from generation to generation. We want to show that the law is true. Consider the simple case of only two alleles, A and B , in a gene. The probability of occurrence of the A gene in a population in generation n is p_n , and that of the B gene is q_n . $p_n + q_n = 1$. These two alleles combine to form

in the next generation AA or BB or AB , with probability p_n^2 , q_n^2 , and $2p_nq_n$, respectively.

- a. The probability of the occurrence of the A alleles in the $n + 1$ generation is denoted by p_{n+1} and that of the B alleles by q_{n+1} . We write

$$p_{n+1} = f(p_n, q_n), \quad q_{n+1} = g(p_n, q_n).$$

Find the functions f and g .

Hint: The probability of occurrence of AA in generation $n + 1$ from generation n is p_n^2 . The probability is 100% that the individual with the AA gene has the A allele. The probability is only 50% that an individual with the AB gene will contribute an A allele to the next generation.

- b. Show that $f = p_n$ and $g = q_n$, and therefore

$$p_{n+1} = p_n = p \quad \text{and} \quad q_{n+1} = q_n = q,$$

where p and q are independent of n .

4. Logarithmic spiral

Falcons flying to attack their prey on the ground follow a logarithmic spiral instead of a straight line. This is because their eyes are on the two sides of their head, and if they needed to cock their head to keep their prey in their sight it would increase the air resistance. So they fly in a trajectory keeping the same angle, 40° , between its tangent and the direct line to the prey. Show that the requirement of constant angles yields a trajectory that is in the form of a logarithmic spiral, $r = ae^{b\theta}$, where r is the radial distance to the prey and θ is the azimuthal angle.

5. Fractal dimensions

A mathematical way to generalize our intuitive way of defining the number of dimensions is to define it as the scaling exponent d . If you have a square, a two-dimensional object, and you divide its length and width by a scaling factor—say 2—what you obtain is four smaller squares. So, $4 = 2^d$. Solving, we get $d = 2$, and we conclude that the dimension of the square is 2. If you divide a line into 2, you will get two shorter lines: $2 = 2^d$. So the dimension of the line is 1. Similarly $d = 3$ for a cube. Now consider the fractal shape called the Sierpinski triangle (Figure 1.14). It is constructed in the following way: Start with an equilateral triangle of solid color. Connect the midpoints of each of its sides by a straight line. Take out the inverted triangle in the middle

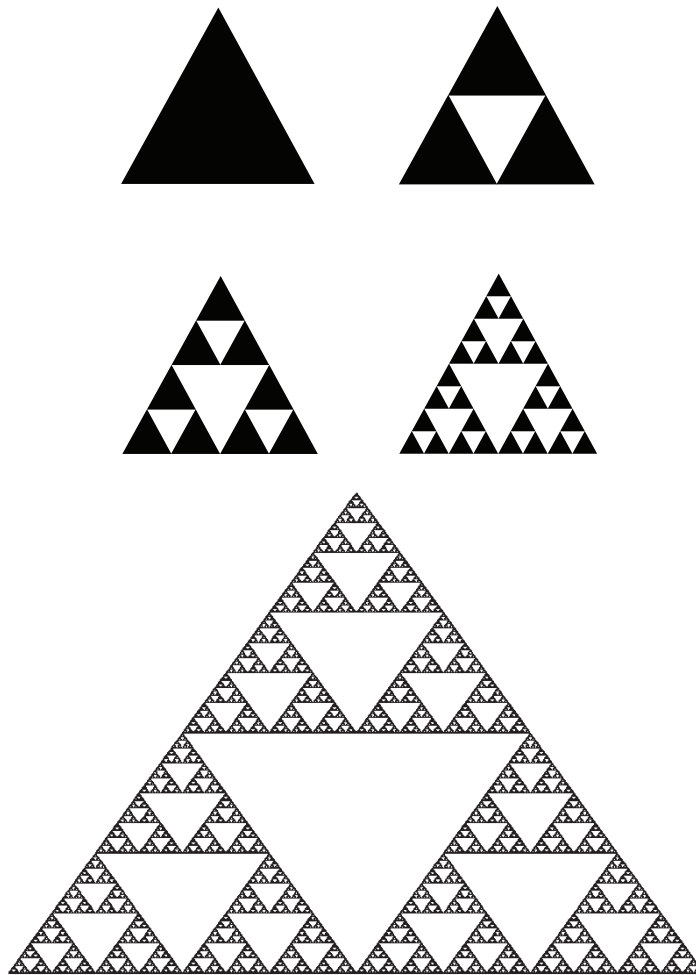


Figure 1.14. The Sierpinski triangle. (Bottom image courtesy of Anthony W. Knapp.)

thus formed. We continue this process with the solid small triangles, until we get the bottom figure in Figure 1.14. What is its dimension? Determine it in the following way:

Divide each of its lengths by 2. How many smaller Sierpinski triangles do you now have contained in the original larger triangle? Set that number to 2^d . Determine its dimension d .

6. Two-dimensional fractal lung and the Golden Tree

The blood vessels in a lung branch into ever smaller capillary vessels to facilitate the exchange of oxygen with the blood carried by the capillary

vessels. One hypothesis is that the resulting form of the branching maximizes the surface area covered by the vessels. We can test this hypothesis with a very simple (and admittedly not too realistic) model of a “lung” in two dimensions. Consider a blood vessel of unit length, which branches into two vessels each of length f , with $f < 1$. The two smaller vessels are 120° apart. Each of them then branches in the same way, with the new branches reduced in length by the same factor f . Repeat this process ad infinitum. We obtain then a fractal tree, which is called the *Golden Tree*. For too small a reduction factor, say $f = 0.5$, for example, you will find that large gaps of space remain that are not covered by the branches of the tree. With too large a reduction factor, say $f = 0.7$, you will find that the branches overlap. Find the optimal f that yields an arrangement with the branches just about to touch. This optimal f turns out to be $1/\Phi$.

Hint: Assume without loss of generality that the original stem of length unity is oriented vertically, and branching occurs at the top point of the stem. By graphing the tree, you will notice that because of symmetry it suffices to find the condition for the main branches to touch horizontally. They in fact touch at a point directly above the first stem. The condition for touching is that the sum of the horizontal projections of all branches with decreasing lengths starting with the branch of length f^3 be equal to the horizontal projection of the large branch of length f . That is,

$$f \cos 30^\circ = f^3 \cos 30^\circ + f^4 \cos 30^\circ + f^5 \cos 30^\circ + \dots$$

Canceling the cosine factor and noting that the right-hand side is a geometric series that you can sum up exactly, you will find an algebraic equation for f .