

CONTENTS

<i>Preface</i>	xi
INTRODUCTION	1
PART I. Who Noticed First?	19
CHAPTER 1. The (So-Called) Fibonacci Sequence in History	21
CHAPTER 2. Plant Patterns in Leonardo's Notebook	34
CHAPTER 3. The Golden Ratio as a New Year's Gift	41
PART II. Could Early Scientists Explain Plant Spirals?	51
CHAPTER 4. First Spirals in the Dew	53
CHAPTER 5. Biomathematics on a Watch Face	68
CHAPTER 6. So Many Spirals on a Pinecone	78
CHAPTER 7. Irrational Angles in a French Garden	96
PART III. What Did the Microscope Reveal?	117
CHAPTER 8. A Glimpse of the Growing Tip	119
CHAPTER 9. Biomechanics under the Lens	129
CHAPTER 10. A Critical Tree on Graph Paper	142

PART IV. Have Computers Shed Any Light?	159
CHAPTER 11. Sunflowers on Turing's Primitive Computer	161
CHAPTER 12. Leaves and Petals as Data Points	175
CHAPTER 13. The Big Experiment with Tiny Droplets	183
CHAPTER 14. Zigzag Fronts in an Artichoke	201
CHAPTER 15. Self-Repeating Patterns in Plants (Perhaps?)	219
CHAPTER 16. Leaf Bud <i>Kirigami</i>	233
PART V. What Do Biologists Think?	245
CHAPTER 17. The Hormone That Makes Spirals	247
CHAPTER 18. A Cell Division Discovery via Soap Bubbles	254
CHAPTER 19. A Brief Detour to Animals	265
PART VI. Conclusion	275
CHAPTER 20. <i>Do Plants Know Math?</i>	277
CHAPTER 21. A Spiral Dinner (with Recipes)	281
<i>Appendix</i>	289
<i>Notes</i>	309
<i>Illustration Credits</i>	327
<i>Acknowledgments</i>	331
<i>Index</i>	333

INTRODUCTION

Phyllotaxis is an adventure in curiosity. It will lead you on a journey into the wild world where nature meets numbers. You will discover in the pages of this book (if you don't already know) that your life is surrounded by botanical sequences and spirals, and that they are very beautiful.

Along the way, you may find that

- ⊗ You start seeing patterns in such everyday items as strawberries, pineapples, corn, red cabbage, and artichokes.
- ⊗ When walking in the woods, you become mesmerized by pinecones.
- ⊗ You catch yourself counting 1, 1, 2, 3, 5, 8, 13, 21, . . . on a regular basis and finding in that a kind of thrill. Amazingly, the Fibonacci sequence—obtained by adding together the last two numbers to obtain the next one—appears in a vast number of plants.

This will be no dry scientific treatise, but instead a very human adventure. In this book, you will delve into the hearts and minds of scientists who have unlocked the secrets of “plant-mathematics” over the course of several centuries. Leonardo da Vinci makes an appearance, and so does Alan Turing. Less famous but equally fascinating is Auguste Bravais, a French naval officer who explored the Arctic. He discovered mathematical forms in both plants and crystals, only to succumb at an early age to an acute form of despair.

Turing, known for his breakthroughs in early computer science, did research on phyllotaxis. From a young age, he was drawn to “watching the daisies grow,” seeking to understand why Fibonacci numbers occur in them. Investigating phyllotaxis was Turing’s last, unfinished work, when he committed suicide under somewhat mysterious circumstances at 41.

As you might imagine, the act of *looking* is crucial to the study of phyllotaxis.¹ (The term, by the way, comes from the Ancient Greek words for “leaf arrangement.”) Observing became a kind of extreme sport for some of the scientists in this book, who had superhuman powers of patience. Alexander Braun, a German botanist, examined the scales on hundreds of pinecones to prove his hypotheses on spirals. The drawings of pinecones that his sister made for him—some with every single scale hand labeled—are exquisite. As for Bravais, the naval officer, he and his brother painstakingly recorded the leaf angles observed in dozens of different wildflowers, from prickly teasels to yellow asphodels. As you will see, their delicate illustrations are equally dazzling.

Over time, the nature of scientists’ phyllotaxis observations changed dramatically. As technology improved, scientists in the late nineteenth century began seeing plants not as static objects but as dynamical systems. They saw that as plants grow, their new leaves and petals do not fit predetermined patterns but instead develop where there is room for them, given limited options for placement. Understanding why this occurs—on a biological and physical level—is eye-opening.

This book intends to introduce you to some math (as far as you dare go), to offer you a peek into scientists’ lives, and to give you a sense of how science works over the course of generations. Sometimes we assume that science proceeds in a neat linear way, always progressing toward Truth. But in reality, science is often messy, and scientists sometimes squabble among themselves and forget what has already been discovered long before. Plants display self-repeating patterns, and science, too, can be self-repeating.

Finally, it’s worth mentioning that phyllotaxis is science, not mysticism. Plants don’t grow in spirals because there is a goddess who loves spirals, or

because aliens brought the golden angle to Earth. Phyllotaxis is based on hard data, and it can get technical—but it can also knock your socks off. The quest to understand why Fibonacci numbers appear in plants is an eminently satisfying one, located at the intersection of math, physics, and biology.

Now, here is where knowing a bit of French comes in handy. (Note that three of the coauthors are francophones: two from France and one from Québec.) Sometimes, French has a word that English simply cannot capture. *Le merveilleux* is one of those terms. Any attempt at an English translation sounds awful. The marvelous? The wondrous? Blech.

Perhaps French is better at conveying emotions than English, and an encounter with *le merveilleux* is always very moving. You bump into something that seems unbelievable yet is entirely real, something that opens your eyes to patterns you never saw before. There is pleasure in discovery, and you never see the world the same way again.

Musings on Math

At first glance, no one would connect plants to math. Plants are from the everyday world all around us. We love seeing them on our walks through gardens, fields, and forests, and we even bring them into the strange habitat of our homes. There, if we remember to water them, they cheer us up. So we love plants, but—perhaps just as with the people we love and live with—we don't really look at them.

Math, by contrast, appears to be from another world. Some say it is a pure creation of our brains. Others argue that math has an actual existence, somewhere out there in an abstract world.

So how exactly do we connect plants with math? Math gets pulled down to our everyday world because of its usefulness. And this usefulness is deeply imprinted in our brains. Many animals have a rudimentary sense of numbers and magnitude. Scientists have detected the neurons used by mud-brown frogs to count the “chuck” sounds in their mating calls. The male with more chucks wins over the female. Ravens can match objects having the same area and perimeter.²

Other examples abound. In humans, this evolutionarily useful sense of basic numbers and magnitude then led to developing more sophisticated values for trade, the measuring of surfaces and volumes, the computing of taxes, and so on. Math can also send people into space. All this is very useful.

But applied to plants? Well, of course we can use math for such practical tasks as predicting or measuring the size of a crop. Yet we can also go much further, applying math to living matter in ways that have nothing to do with conventional ideas of usefulness. That's where the beauty of both math and plants unfurls before our very eyes.

Let's take a look:

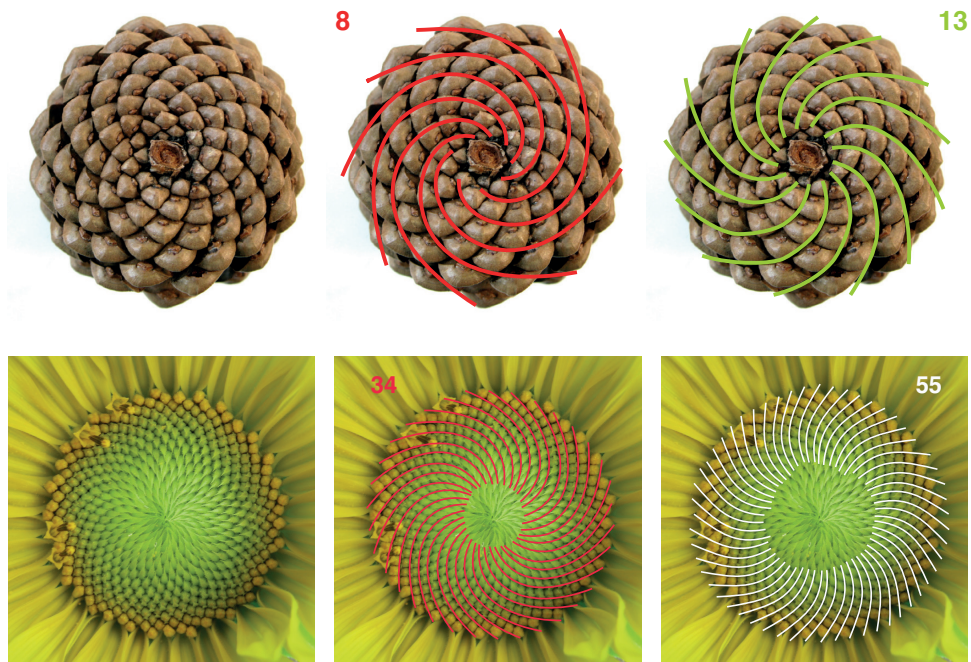


FIG. 0.1 Spirals turning two directions, in pinecones and sunflowers.

On the pinecone and sunflower shown here, we have drawn spirals in two directions. We'll even count them for you: on the pinecone, there are 13 spirals

turning in one direction and 8 in the other; and on the sunflower there are 34 and 55 spirals. These are precise numbers, all of them belonging to the Fibonacci sequence. (Recall that it begins 1, 1, 2, 3, 5, 8, 13, 21, . . .) We will see that this is quite a general property, not special to just the two examples shown here.

So why do these numbers appear? They don't do anything useful for us, and in fact we barely notice them. Are these numbers useful in some way for plants?

And why do plants display these particular mathematical numbers? Are they doing math? Were they doing math before humans began doing it? Did plants help us figure out math? These are the questions we are going to explore in this book, along with stories of the discoveries and the discoverers.

Phyllotaxis in 10 Terms

This book is mostly about spirals. Before you can analyze them, however, you need to learn how scientists see them.

Like all sciences, the study of plant patterns has a specialized vocabulary—and admittedly some of the words are tongue twisters. What follows is a brief introduction to how scientists talk about this fascinating topic at the intersection of biology, mathematics, and physics.

1. SPIRALS

If you're looking at, say, a pinecone, the *spirals* formed by the scales are easy to see. You've probably known about them ever since you were a kid. The aloe plant in figure 0.2 makes it very clear.

Spirals can appear in a variety of contexts in plants, whether in the scales on a pineapple, the leaves of an artichoke, or the florets at the center of a dahlia. Spirals can also appear in the placement of leaves along a stem. It's helpful to think of tracing the thread on a screw, imagining leaves sprouting at equal intervals.

Some scientists have explained Fibonacci phyllotaxis as a way for plants to maximize sun exposure on their leaves, with minimal overlap. The authors of this book find that argument unconvincing, however. Although the sun is rarely directly overhead in most places on Earth (but instead inclined according to the



FIG. 0.2 This plant is known as the “spiral aloe” for obvious reasons.

season), most plants still grow straight upward. In addition, there are many plants whose leaves grow directly above one another—such as the whorled plants described below—yet they have survived natural selection and continue to thrive. And finally, leaves can easily move toward the light to get more sun, as you can see in any houseplant growing in a window.³

2. PARASTICHY NUMBERS

What you may not have noticed is that you can often see plant spirals turning in two directions.

Scientists call each spiral a *parastichy* (while we pronounce this PAIR-a-sticky, others say pa-RAS-ticky).⁴

Usually, scientists count the spirals in both directions and talk about them as a pair (m, n) . These are known as *parastichy numbers*. In this book, we will call the smaller number m and the larger number n .

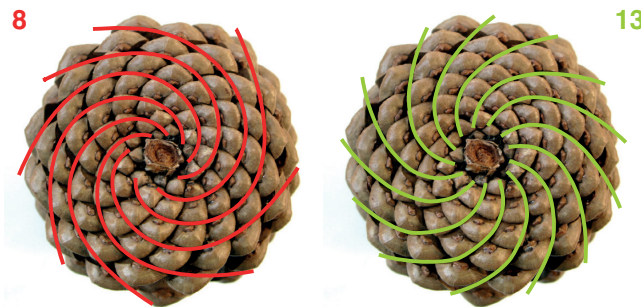


FIG. 0.3 The parastichy numbers for this pinecone are $(8, 13)$.

3. FIBONACCI SEQUENCE

In a beautiful example of how nature meets math, the number of spirals on plants often fits the *Fibonacci sequence*.

The sequence is named after one of its popularizers, an Italian mathematician born in 1170. He was proposing a playful way to describe reproduction in rabbits. As it turns out, the sequence has little bearing on rabbits, but it's quite powerful for plants.

The Fibonacci sequence begins with two pairs of rabbits, 1 and 1. These get added together: 2. Then you simply keep adding the last two numbers to generate the next one: $(1, 1, 2, 3, 5, 8, 13, 21, 34, 55, \dots)$.

Although the sequence is infinite, in the plant world it rarely appears beyond 144. The exception is a large sunflower head, which might have 233 spirals.

Note that in the pinecone in figure 0.3, both parastichy numbers—8 and 13—are Fibonacci numbers.

4. DIVERGENCE ANGLE

Scientists are also very interested in the angle between two consecutive leaves or petals (meaning that one grew after the next). This is called the *divergence angle*.

When plants display spiral phyllotaxis, one leaf does not grow directly above the next. Instead, the divergence angle between two leaves is often close to 137.5° . This is famously known as the golden angle.

Remarkably enough, as we will see, the golden angle is closely connected to the Fibonacci sequence.

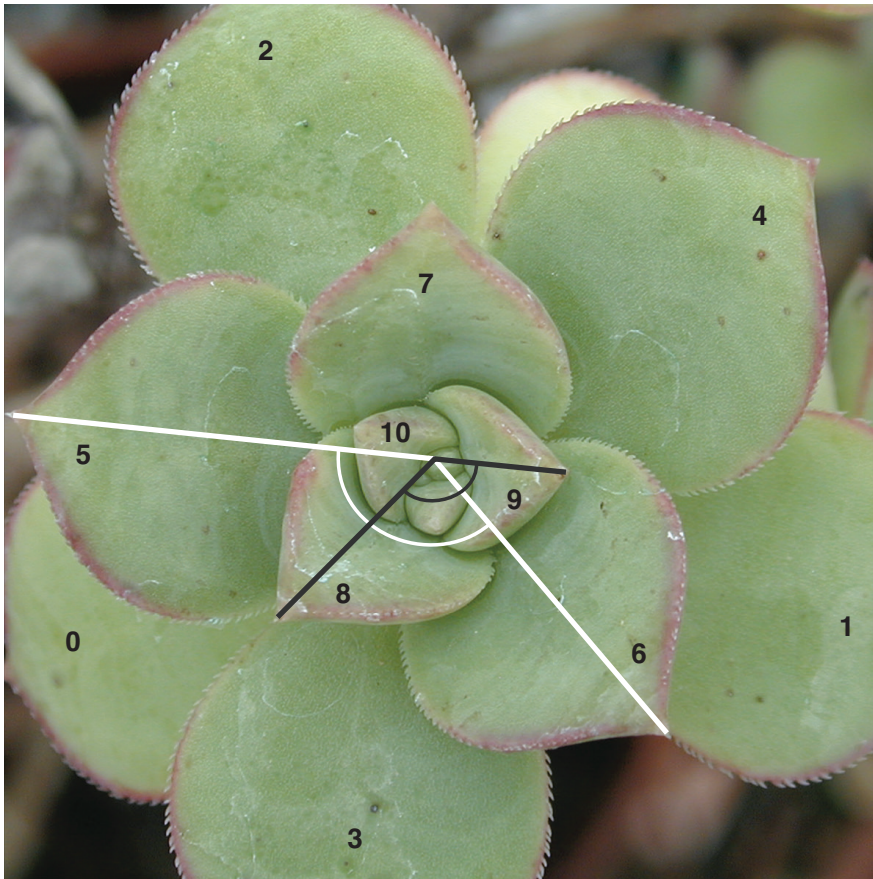


FIG. 0.4 Leaves in this *Aeonium* are numbered according to age. The divergence angle between leaf 8 and leaf 9 is shown in black, and that between leaf 5 and leaf 6 in white. Both are close to 137.5° .

5. GENERATIVE SPIRALS

Another useful tool imagines a spiral joining consecutive leaves along the length of a plant stem. This is called a *generative spiral*.

The beauty of the generative spiral is that it makes it easy to determine the average divergence angle between two leaves. To do this, first find two leaves growing almost directly above each other. (See the blue leaves indicated in fig. 0.5.) Then follow the generative spiral linking one leaf to the next. Count the number of leaves between the lower leaf and the upper one—but don't count the leaf you started with. Now count the number of full turns you made around the stem. The ratio of these two numbers gives you the average divergence angle.

Try this using the plant drawing in figure 0.5 at left, traveling between the two blue leaves:

$$\# \text{ turns} / \# \text{ new leaves} = 5 \text{ turns} / 13 = 0.385 \text{ turns} = 138.5^\circ$$

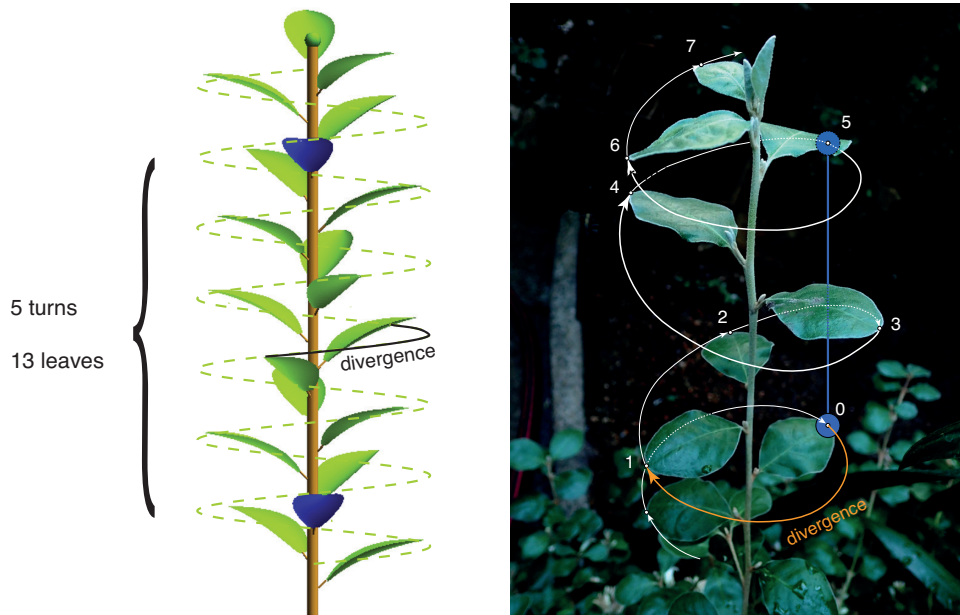


FIG. 0.5 At left, the dotted line indicates the generative spiral. At right, this spiral is shown by a white line winding around the plant. Note that the leaves marked in blue are almost perfectly aligned.

Note that this angle is close to the golden angle of 137.5° . (We will often return to this famous angle, starting in chapter 4 on the Bravais brothers.)

Now look at the second example, figure 0.5, right. Note that the leaves are numbered according to age, with older leaf 0 located almost directly below younger leaf 5. Following the white generative spiral, you make about two full turns to travel from one leaf to the other. And so, in this case, the average divergence angle is roughly

$$\# \text{ turns} / \# \text{ new leaves} = 2/5 \text{ turn} = 2/5 \cdot 360^\circ = 144^\circ$$

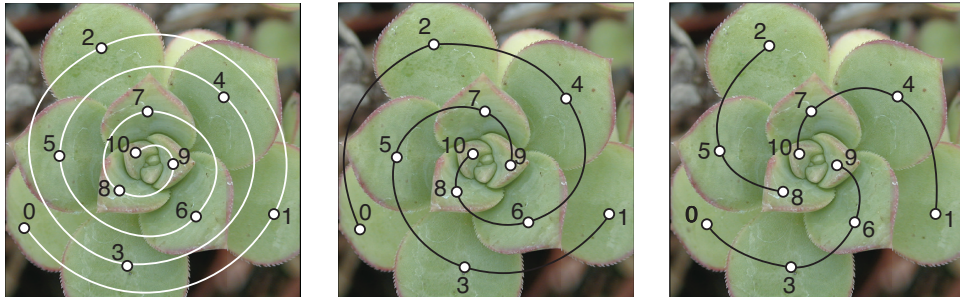


FIG. 0.6 Three spirals are shown on the same *Aeonium*: at left, the white generative spiral passes through each leaf, generation by generation. The middle and right-hand photos show 2 counterclockwise parastichies and 3 clockwise parastichies, so the plant's parastichy numbers are (2, 3).

6. LATTICES

In addition to photographing and labeling actual plants, scientists have developed systems for modeling their geometry. Among the most useful are *lattices*.

Lattices show each leaf (or other plant organ) as a disk, in order to more clearly demonstrate plant patterns. (Well, technically the earliest lattices in botany used points instead of disks.)

In figure 0.7, the left-hand image is a *spiral lattice*, which views the plant from the top down.

The right-hand image is a *cylinder lattice*, which views the plant stem as if rolled out flat.

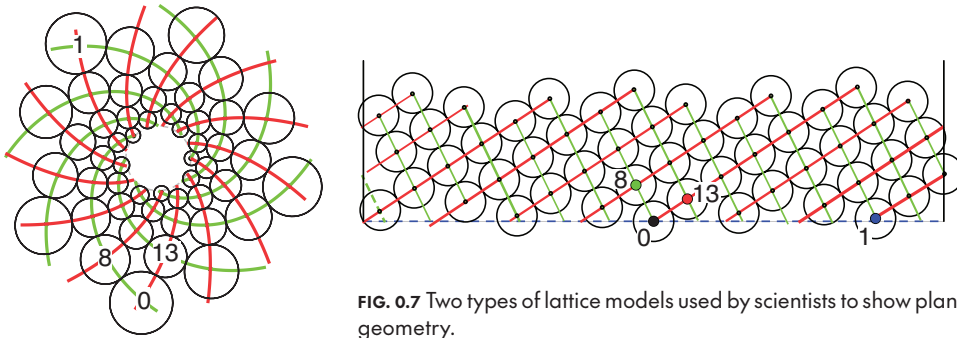


FIG. 0.7 Two types of lattice models used by scientists to show plant geometry.

7. PRIMORDIA

Observing the formation of plant spirals, scientists study new plant organs as they emerge. When a new organ first emerges as a bump that will become a leaf, petal, scale, or other part, it's known as a *primordium*. The plural is *primordia*.

By using the word “primordia,” scientists can speak about new plant organs in general, rather than being limited to particulars.

8. MERISTEMS

Given that most plants grow in spirals, how exactly does this occur? Scientists look closely at the very tip of the growing stem, around which the primordia appear.

The plant's tiny “organ factory” is called the *shoot apical meristem*. Scientists sometimes refer to this as the SAM.

Usually invisible to the naked eye, a SAM is best seen through a scanning electron microscope, or SEM. It's here that cell division takes place. Figure 0.8 is a SAM viewed by a SEM. The entire image of the meristem is about 1 mm (1/24 of an inch) and would fit on a pinhead.

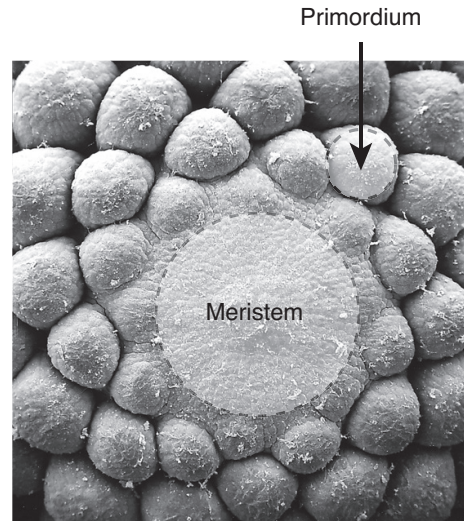


FIG. 0.8 Scanning electron microscope (SEM) image of the shoot apical meristem of a spruce branch, surrounded by needle primordia.



FIG. 0.9 Whorled phyllotaxis in a great horsetail (*Equisetum telmateia*).

9. DYNAMICAL SYSTEMS

For centuries, scientists saw phyllotaxis as static. They observed dried plants, preserved at a single moment of their existence.

Only in recent decades has phyllotaxis been understood as a *dynamical system*, a mathematical model that describes movement over time. Plant spirals are not static but instead emerge as a function of cell division and plant growth.

10. WHORLED PHYLLOTAXIS

While the majority of plants in nature exhibit spiral phyllotaxis, other growth patterns do exist. Among them, the most common is called *whorled*.

In whorled phyllotaxis, multiple organs grow at each level of the stem. In the ancient plants called horsetails, as many as 20 leaves can be found on a single level.

ONE MORE . . .

One additional type of phyllotaxis, studied in detail by this book's authors, is the *quasi-symmetric phyllotaxis* found in such plants as strawberries and corn. Although these display some regularity that can be analyzed mathematically, the patterns are not as predictable as in plants displaying classic Fibonacci phyllotaxis.

Try Your Hand

Draw Smartphone Spirals

1. Take a photo with your smartphone of a flower whose spirals are very clear. If you're lucky, you might find this out in nature. Or else in a garden shop. Alternatively, take a photo of a flower in this book, like the dahlia in figure 0.10.
2. Using the edit function, click on the markup (or drawing) function. Choose a bright color for contrast and use your finger to trace all the clockwise spirals. Tip: don't try to draw spirals across the whole flower, only where they are most obvious—usually toward the outside. The center can get messy.
3. Take a screenshot.
4. Revert to the original photo. Now, using a different bright color, trace all the counterclockwise spirals. (In the dahlia, the counterclockwise ones are harder to see.)

Did you end up with (m, n) parastichies that are Fibonacci numbers? Hopefully *oui*! (This technique also works with pinecones.)

Pin Pineapples

Pineapples display spirals running in two directions, often with a clear dominant side (i.e., some pineapples are left-handed, and some right-handed). Using colored pushpins is the easiest way to see and count the spirals. You may reach dead ends, where the spirals divide. These are “transitions,” which we will explore in later chapters.

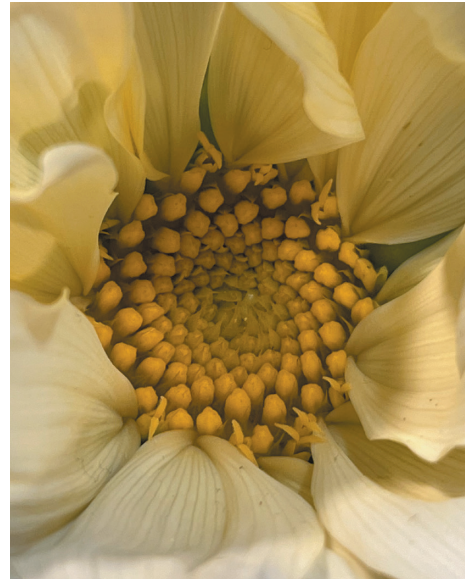


FIG. 0.10 A dahlia, useful for drawing and numbering spirals.

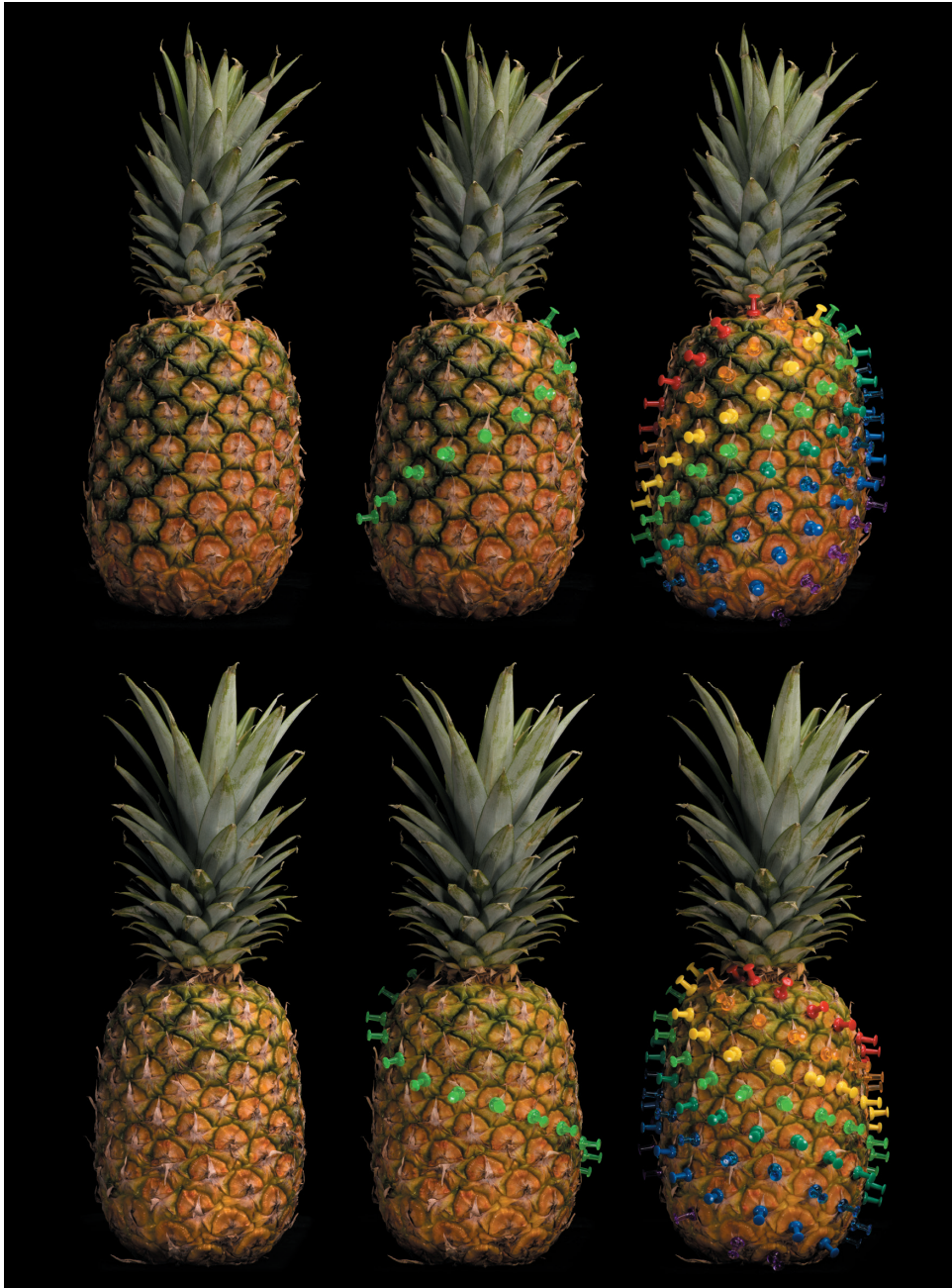


FIG. 0.11 Colored pushpins make it easy to count spirals on a pineapple.

Roll Your Own Cone (3D to 2D)

In this activity, you will “unroll” a plant cone on dough. This is a good way to observe and count the plant spirals that wrap all the way around the cylinder.

1. Unrolling Your Cone

- a. Find a pinecone or other cone that’s fairly symmetric. Here, we have used a nice closed cone from a black pine (*Pinus nigra*). (You can make your cone close up by leaving it in a humid environment.) Your cone should show clear, tight spirals and be firm enough to leave an imprint when rolled.
- b. Roll out some dough or modeling clay using a rolling pin (or a bottle). Your slab should be about the thickness of pie dough. Make it a little wider than your cone and with a length about eight times its diameter.
- c. On your cone, mark a point midway between the top and bottom, using a blob of paint or nail polish. This will mark one full turn of your cone.
- d. Roll out your cone onto the dough, using the fingers on both hands to go as straight as possible. Apply firm and constant pressure. Roll at least two full turns of the pinecone.
- e. Check to make sure your paint mark shows up for each full turn.

2. Tracing and Counting Parastichies

- a. Choose a pair of consecutive marks on your imprint.
- b. With your finger, trace the parastichy that passes through the left-hand mark and slants upward, following the lines between the scales. This will be 1.
- c. Next, trace and count the parastichies that run parallel to the first one.
- d. Stop counting when you reach the parastichy *before* the one that passes through the right-hand mark. We got 5 for our pinecone.
- e. Repeat the process, this time using the parastichies slanting downward. We got 8 for our pinecone.
- f. Sometimes your cone, like ours in the picture, will show transitions—places where some parastichies split or come to a dead end. First, focus on the part of the slab with a regular pattern.

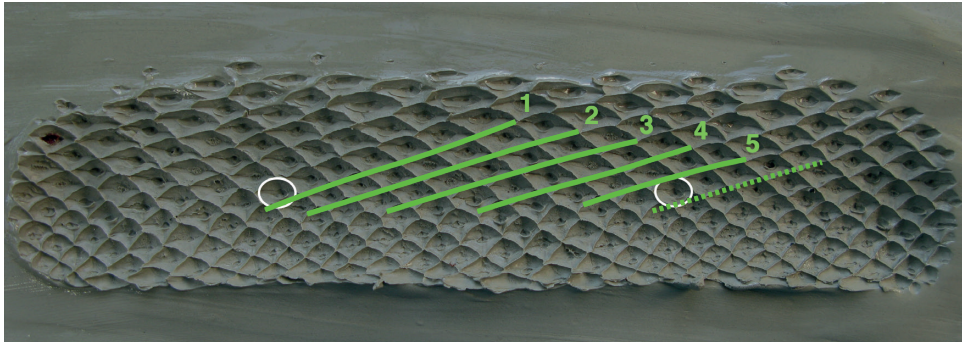


FIG. 0.12 Tracing the first set of parastichies.

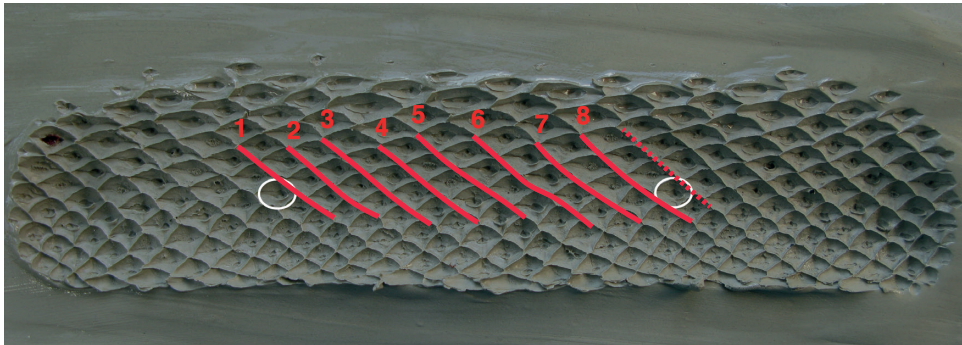


FIG. 0.13 Tracing the second set of parastichies.

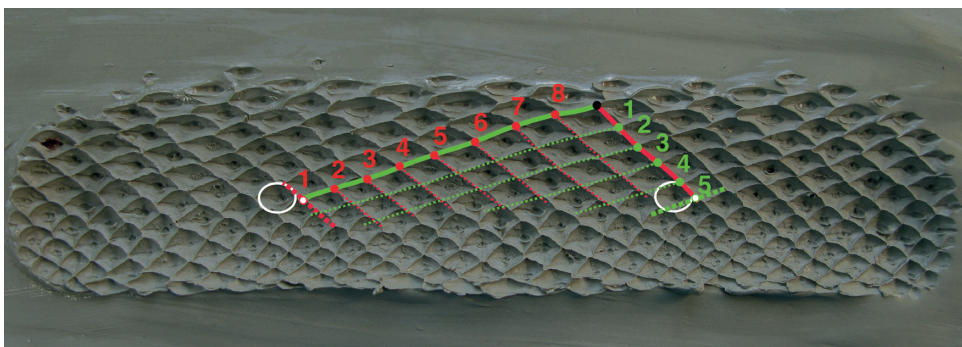


FIG. 0.14 Counting the steps reveals the parastichy numbers.

- g. Can you also count the steeper, upward-slanting parastichies in the lower part of our cone? (It should come as a nice surprise). Do you notice any change in the number of downward parastichies?
- h. Another approach is to trace one parastichy going up from a chosen point and another going down through the same point one full turn later. (These are the same points on the pinecone, meeting when you complete the turn.) If your imprint is wide enough, these lines will cross (shown in fig. 0.14 as a black dot), forming a triangle. Count the number of steps going up to that intersection and then the number going down. In the photo, we go up 8 (green) steps. At each of these steps, we cross one red, downward parastichy. So the number of steps on the *green* line equals the number of *red* parastichies. Likewise, going down the *red* line, you can count 5 steps, each crossing a *green* parastichy. So the number of green, upward parastichies will be 5.

INDEX

- acorn caps, 203, 218
Adanson, Michel, 239–40; portrait of, 240
Adler, Irving, 196–98
aloe plant, 5, 6
alternate phyllotaxis, 58, 72
alternation of generations, 119–21
animals, 265–73
Anthurium, 135, 209, 213, 279
apical meristem: microscope images of, 11, 121–26, 205–6, 208; mother cell of, 261, 263; Turing’s analysis of, 168, 169. *See also* meristem
Araceae family, 135–38, 218, 278–79
Archimedean spirals, 32, 86, 315n8(Ch.6)
artichokes, 205–7, 283
asparagus, 284
Atela, Pau, 204, 320n1
attractors, 261, 263
auxin, 251–53

Banksia, 217
Besson, Sébastien, 259
bifurcations: broken, 194; of cylindrical protein lattices, 250; Van Iterson diagram and, 181–82, 194–96, 320n5
bijugate phyllotaxis, 137, 303
biomechanics of plants, 131–32

Bonnet, Charles, 53–66; on dew, 54–57, 58, 312n6, 312n8; exceptions to leaf orders of, 63–64, 292–94, 313n22; five leaf orders of, 58–66; portrait of, 54; Schimper inspired by, 69, 70–72
Bonnet syndrome, 64
Braun, Alexander, 68–69, 72, 76–77, 78–90; discoveries of, 112–13. *See also* Schimper and Braun’s spiral theory of phyllotaxis
Braun, Cecilie, 79–81, 88; portrait of, 79
Bravais brothers: discoveries of, 112–13; fieldwork of, 106–8; golden angle and, 88, 96–97, 100–103, 106–10, 112, 149; illustrations drawn by, 100–101, 103–4; lattices of, 103–6, 180, 182, 315n7; lives of, 96–99; portrait of Auguste, 97
Bravais lattices, in crystallography, 97, 110, 112, 278
buds: apical meristem of, 122–24, 168, 169; cabbage as, 234–35; packing of leaves inside, 127–28, 233–43, 273, 323n2; of radish, 86, 88; Turing’s analysis of growth in, 168, 169
bur chervil, 226, 227, 231

cabbage, 215–16, 234–36, 282
Calandrini, Jean-Louis, 54, 58, 59, 62, 64, 312n16

- camera lucida, 137
- Cantor, Georg, 220–21
- Cantor set, 221, 224
- cell division, 254–64
- cell walls, 256
- chemical morphogenesis, 164–66, 168, 169
- Church, Arthur Harry, 145, 156–57
- climate, and leaf shape, 239
- computer simulations: disk stacking in, 129–30, 134, 136, 205; finding parameters in, 192–99; Lindenmayer’s early results, 176–79; Snow and Snow hypothesis in, 303; Turing’s first for phyllotaxis, 165
- contact pressure, 139–41, 182, 187, 252–53
- continued fractions, 68, 105–6, 108–10
- corn, 12, 64, 200, 203, 216, 292, 321n6
- Couder, Yves, 170, 183, 186–87, 189, 191–92, 198, 204
- Couturier, Etienne, 233–34, 238–39
- cylindrical (cylinder) lattice, 10–11, 112, 249–50
- dahlia, 13, 92–95
- Darwin, Charles, 272–73
- decussate phyllotaxis, 38, 58
- deformation, 132, 139–41, 182. *See also* contact pressure
- disk diameter: quasi-symmetric patterns and, 216–17; Van Iterson diagram and, 147, 153–54
- disk lattices. *See* lattices
- disk stacking, 129–30, 133–36, 149, 155, 176, 205, 316n12. *See also* rhombic tilings
- divergence angle: of Braun’s pinecones, 82–83, 84–86, 314n6; in cell division model, 262; coined by Schimper, 69, 112; constant and irrational, 102–6; defined, 8; generative spirals and, 9–10, 104–6; as quotient of Fibonacci numbers, 72–76; rational for Schimper and Braun, 102–3, 149; in Schimper’s watch face model, 70–72; Van Iterson diagram and, 147, 149, 262. *See also* golden angle
- divine proportion, 45, 49. *See also* golden ratio ϕ
- dodecahedron, 45, 48
- Douady rabbit, 224–25, 307
- dynamical systems, 12, 126, 166, 187–88, 195–97, 261
- empiricists vs. idealists, 247–48, 250–51
- energy in Levitov’s analysis, 179–81, 299–300, 320n10
- Erickson, Ralph O., 250
- Errera, Léo, 255–56, 257–58, 259, 260, 264; portrait of, 256
- Farey sequence, 278, 294, 295
- ferns: alternation of generations, 119–20; apical cell of, 263; Archimedean spiral and, 32, 33
- Fibonacci (Leonardo de Pisa), 24–28
- Fibonacci numbers: in Bonnet’s observations, 63–64; defined, 7; divergence angles as quotients of, 72–76; sunflowers not conforming to, 172; in Van Iterson’s diagram, 149–50. *See also* parastichy numbers
- Fibonacci poem, 77, 309n1(Ch.1)
- Fibonacci sequence, 1; of bee drone ancestors, 31; defined, 7; golden ratio and, 45–46, 48, 311nn5–6; of Indian poets, 28–30; Kepler and, 41, 45–46, 48; Leonardo de Pisa and, 24–28; in rabbit problem, 26–28
- Fibonacci spirals: in animals, 266, 271; functional significance of, 273, 325n16; hands-on activities, 31–33, 65–67; in magnetic droplets, 190–91; transitions between, 155
- fir trees, 39–40, 141
- flowers: five-petaled, 41, 43–44, 46; labeling floret numbers, 92–94

- formation, and Schwendener's biomechanics, 132, 139, 182
- fractals, 219–24; in plants, 224, 226, 231–32.
See also self-similarity
- fraction trees, 74–75, 84–86, 294–96
- fundamental hypothesis of phyllotaxis, 180–81, 319n10
- Fundamental Theorem of Phyllotaxis, 103
- generative spirals: of Bravais brothers, 104–6; defined, 9–10; left behind by Hofmeister's rule, 133; Schimper's construction of, 72, 112
- Goethe, Johann Wolfgang von, 120, 122
- golden angle, 8, 47; Bravais brothers and, 88, 96–97, 102–3, 106–10, 112, 149; continued fractions and, 108–10; as divergence angle, 8, 100, 102–3, 108, 149; hands-on activity, 113–15
- golden mean. *See* golden ratio ϕ
- golden ratio ϕ , 45–49; Bravais brothers and, 110; Kepler and, 41, 42, 46; myth about, 48–49; renormalization and, 155
- golden section. *See* golden ratio ϕ
- grasses, 38
- Greece, Ancient, 22
- growth parameter, 192–94
- Hakim, Vincent, 194
- Han Ying, 22
- helix (helices), 58, 62, 66, 72, 81, 309n4(Intro.)
- Hemachandra, 28–29
- hexagonal lattices: in evolution, 273; Levitov and, 180, 299–300; in transitions, 306; in Van Iterson tree, 149–51, 318n10, 320n8
- hexagonal packings, 149, 180, 273, 299. *See also* hexagonal lattices
- hexagonal patterns in animals, 265, 267–70, 324nn5–7(Ch.19)
- Hofmeister, Wilhelm, 119–28, 277; portrait of, 121
- Hofmeister's rule, 122, 124–26; disk stacking and, 133–34; empiricists' use of, 248; magnetic droplets and, 188, 198; transitions and, 212
- honeybee drone genealogy, 31
- horsetails, 12
- Hotton, Scott, 204, 305, 320n1
- hyperbolic geometry, 308, 317n9, 326n17
- icosahedron, 45
- idealists vs. empiricists, 247–48, 250–51
- Indian poets, 28–30
- inhibitor, and pattern formation, 164–65, 176–77, 251–53
- irregular cases, 278. *See also* quasi-symmetric phyllotaxis
- Kepler, Johannes, 22, 41–44, 290–91; portrait of, 42
- kirigami*, 233, 235, 238, 241–43
- Koch snowflake, 222–23, 224
- lattices, 10–11; of Bravais brothers' phyllotaxis, 103–6, 180, 182, 315n7; of Bravais crystallography, 110, 112; in Schwendener's deformation model, 139–41; of Van Iterson, 146–50, 153–55
- leaves folded in buds, 127–28, 233–43, 323n2(Ch.16)
- Leonardo da Vinci, 34–40, 45, 49, 311nn5–7; quincunx and, 38, 58; trees and, 39–40, 289–90, 325n2
- Leonardo de Pisa. *See* Fibonacci
- Levitov, Leonid S., 179–82, 185, 187, 194, 195–98; energy and, 179–81, 299–300, 320n10
- lichens, 130–31
- Lindenmayer, Aristid, 171, 176–79, 226, 228
- logarithmic spirals, 32, 33, 271
- L-systems, 127, 156, 176, 178, 228, 319n2
- Lubbock, John, 240
- Lucas, Édouard, 28

- magnetic droplets, 182, 187–91, 198
magnolias, 135–36, 137
Mandelbrot, Benoit B., 223–24
Mandelbrot set, 204, 224, 225, 304–05
mediant, 75, 79, 86, 108–9, 294–96
meristem, 11; Hofmeister’s rule and, 248;
 optimal packing in, 273; zigzag fronts and,
 208–9. *See also* apical meristem
microscope: apical meristem and, 11, 121–26,
 205–6, 208; cell division and, 257; Hof-
 meister and, 120, 121–24; Schwendener
 and, 129, 130–31, 133, 137
microtubules, 263–64
mollusks, spirals in, 32–33, 270–71
morphogenesis: chemical, 164–66, 168, 169;
 growth history and, 198; patterns emerg-
 ing from, 277
myrtle, 22, 23, 60

Nägeli, Carl von, 121–22
Nagpal, Radhika, 261
natural selection, 272–73
nautilus shell, 33

orthostichies, 84–85, 86, 112, 326n11. *See also*
 vertical spirals

parastichy: Braun’s introduction of, 81;
 defined, 7
parastichy numbers, 7; as adjacent Fibonacci
 numbers, 108; Braun’s introduction of,
 83; in computer simulations, 179, 192–93;
 counting for yourself, 13–17; double
 Fibonacci numbers in, 137; with magnetic
 droplets, 189–91; nearly equal, 216–18;
 relatively prime, 95, 105; starting at (1,1)
 or (2,2), 214–15; Turing’s observation of,
 166–67; Van Iterson diagram and, 146–50;
 zigzag fronts and, 209–10. *See also* transi-
 tions in parastichy numbers
peace lily, 135, 210–11, 212, 218, 279

pentagons, 45–48; in Bonnet’s quincunx order,
 62; in ommatidia pattern, 270; transitions
 and, 203, 211–12
petai, 217
photosynthesis, 53, 57
phyllotaxis: coined by Schimper, 69; duality
 of Fibonacci or quasi-symmetric, 218; era
 of fixed geometry, 112–13; Greek for leaf
 arrangement, 2, 69
pineapples, 13–14, 281
pinecones: Braun’s work on, 76–77, 78–87,
 112, 296–99, 314n6; counting spirals in,
 4–5, 7, 15–17, 111, 186; divergence angles
 of, 82–83, 84–86, 314n6(Ch.6); numbering
 scales of, 80, 81, 83; radial view of, 86–87;
 vertical spirals in, 82–83, 84, 112
Plantefol, Lucien, 187
Plateau, Joseph, 255–56
Pliny the Elder, 22, 24
primordia, 11, 122–26; added singly by simple
 rules, 176; bifurcations and, 194–96;
 formed in L-systems, 176–77; Hofmeister’s
 rule and, 122, 124–26; Schwendener’s disk
 stacking and, 133–35; Turing’s analysis of,
 164–66, 168–69; Van Iterson diagram and,
 147, 149, 153, 155; zigzag fronts and, 208–9
protein crystals, 248–51
Prusinkiewicz, Przemyslaw, 178–79, 228

quasi-symmetric phyllotaxis, 12, 203, 216–18,
 273, 279
quincunx: Bonnet’s description of, 53, 58,
 61–62; Bonnet’s variations of, 63–64,
 292–93, 313n22; cardboard model of, 65;
 divergence angle of, 72, 74; Leonardo’s
 observation of, 38

rabbit problem, 26–28
recipes, 281–87
redoubled spirals, 53, 58, 62–64, 66, 72
renormalization, 153–55, 278, 308

- rhombic tilings, 205, 321n3
- rhombuses in transitions, 203, 211–12
- rise, 193, 262
- Romanesco broccoli, 183–86; fractal view of, 220, 226, 228–29, 231; recipe for, 285
- Sanskrit poets, 28–30
- Schimper, Karl, 68–77, 78–79, 86; discoveries of, 112–13; portrait of, 69
- Schimper and Braun’s spiral theory of phyllotaxis, 79, 88; Bravais brothers and, 98, 102–3; dismissed by Hofmeister, 121
- Schoute, Johannes Cornelis, 252
- Schwendener, Simon, 122, 126, 129–41; contact pressure theory of, 139–41, 182, 187, 252–53; disk stacking and, 133–34; microscope and, 129, 130–31, 133, 137; portrait of, 131; unusual transitions and, 135–36
- self-similarity: in Church’s art, 156; of Van Iterson’s diagram, 147, 149, 153, 182, 220, 230–31, 307–8. *See also* fractals
- shoot apical meristem (SAM), 11. *See also* apical meristem
- Sierpiński carpet, 221–22
- Snow and Snow rule, 198, 303
- soap bubbles, 254–64
- spiral lattice, 10–11, 299
- spirals in plants, 5–6; Bonnet and Calandrini as first to write about, 53, 62–64; in cabbage leaves, 234–35, 236; Fibonacci spirals, 31–33, 65–67; Leonardo’s observation of, 38, 40. *See also* parastichy numbers; Schimper and Braun’s spiral theory of phyllotaxis
- spruce branch, 208–9
- square lattices, 92, 149–51, 154, 196, 270, 273, 299–300, 306, 318n10, 320n10, 324n5(Ch.19)
- strawberries, 12, 135, 203, 210, 218, 286
- sunflowers: computer-generated, 178; counting spirals in, 4–5, 7, 172–74; dynamic construction of, 198; parastichy numbers of, 108, 215; Turing’s work on, 166–67, 172
- sunlight on leaves, 5–6, 273
- Swinton, Jonathan, 167–68, 170, 172
- sycamore maple, 235, 236, 238, 240
- tangrams, and cell division, 254, 263
- teasels, 135, 137–38
- Theophrastus, 22, 23
- Thompson, D’Arcy Wentworth, 143–44, 256–58, 259, 260
- threshold of dynamical stability, 195–97
- transitions in parastichy numbers, 130, 134–36; in pineapples, 13; Turing’s analysis of, 169–70; Van Iterson’s analysis and, 153–55; zigzag fronts and, 201, 203, 206–7, 210–16
- transitions in quasi-symmetric patterns, 216–18
- trees: leaves folded in buds, 235–40; Leonardo on, 39–40, 289–90, 325n2
- triangle transitions, 203, 210–17, 305
- Try Your Hand: Fibonacci poem, 77; Fibonacci sequences, 31–33; Fibonacci stem, 91–92; golden angle of divergence, 113–15; *kirigami* maple leaf, 241–43; labeling floret numbers, 92–94; parastichies, 13–17; spiral stems, 65–67; Turing’s sunflowers, 172–73
- Turing, Alan, 95, 161–74; chemical patterns and, 164–66, 251; death of, 171; dynamical systems and, 126, 166; hypothesis of geometric phyllotaxis, 170, 180–81, 182; portrait of, 162
- Turing instability, 166
- Van Iterson, Gerrit, 130, 132, 142–56; portrait of, 144
- Van Iterson diagram, 142–43, 146–50; cell division and, 254, 261–62; computer simulations and, 178, 179–81, 193–97; Fibonacci branch of, 149, 150, 155, 179; self-similarity of, 147, 149, 153, 182, 220, 230–31, 307–8

- Veen, Arthur, 176–78
Venus flytrap, 257–60
vertical spirals: in corn, 200; oscillating a little, 314n5; in pinecones, 82–83, 84, 112. *See also* orthostichies
von Sachs, Julius, 247–48; portrait of, 248
whorled phyllotaxis, 12; Bonnet’s observations of, 58; ignored in simple model, 204–5; Leonardo’s observations of, 38, 39–40; noticed by the ancients, 22–24; in Schwendener’s magnolia drawing, 136, 317n13
Wiener, Norbert, 258–59, 263
yellow asphodel, 106–8
Young, John Zachary, 163–64
zigzag fronts: counting parastichies with, 209–10; emergence of, 208–9; transitions and, 201, 203, 206–7, 210–16
zigzag line of Van Iterson, 155, 321n4