View from the Pennines: Phyllotaxis and Fibonacci

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Not a lot is growing at the moment, but I have spiral eyes. I am like a character in an obsessive novel (think Danielewski [1], or Dan Brown [2] if Danielewski is too obscure). I hunt for spirals in the hyacinths and think I find them – though the florets are passed their best and perhaps I see what I want to see. I seek them in the cyclamen stalks (no, probably not) and monitor the molehills (definitely not). I can't wait for the pale blue muscari to appear in spring so I can count the round florets on their conical heads.

And summer will bring the sunflowers.

Figure 1: Sunflower. ©Visceralimage|Dreamstime.com

The sunflower, or more accurately the head of the sunflower flower, has become a symbol for the ubiquity and power of mathematics; the power to describe the living world as well as the physical world. It is a commonplace of popular books on mathematics that the number of spirals in the two families (one family clockwise and the other anti-clockwise) that our eyes pick out in the pattern of seeds on the head of the flower are arranged in Fibonacci pairs, i.e. they are successive terms of the series $1, 1, 2, 3, 5, 8, 13, 21, 34, \ldots$, where each term is the sum of the previous two. The Fibonacci numbers F_k have many beautiful properties, for example the ratio of successive terms F_k/F_{k+1} tends to $g = (\sqrt{5} - 1)/2$, the reciprocal of the golden mean and these ratios are the best rational approximants of the irrational number g. They are also (equivalently) the truncated continued fractions approximants of g. The connection between observed spirals in biology and a significant (hence deep) irrational number have led the sunflower (or a mathematically equivalent flower head) along with the nautilus shell to adorn the covers of books covering broad swathes of mathematics from Frank Land's popular *The Language of Mathematics* [3], which uses a shell and a daisy head in at least one edition, to the weighty *Princeton Companion to Mathematics* [4] (shells again). But the principle is the same.

But is it true? And if it is true, then why is it true?

The answers are 'probably', and 'it depends who you talk to', with some people hedging their bets and considering a variety of possible mechanisms.

It is hard to find good evidence for the Fibonacci connection beyond the anecdotal. My understanding [5] is that the largest trials used around 1,000 heads and found Fibonacci spirals in approximately 80% of these. Of the non-Fibonacci cases, many were double Fibonacci's, $(2F_k, 2F_{k+1})$. So it looks as though there is some experimental basis to the belief that the seeds often (or usually) arrange themselves in families of spirals related by Fibonacci numbers.

The next question is why, and should this be surprising? This is where phyllotaxis comes in. Phyllotaxis is the study of the arrangement (*taxis*) of leaves or buds or seeds (*phyllon*). As a stem develops, leaf buds appear in positions determined by some biological mechanism, forming a pattern around the stem. The same general mechanism governs many growth patterns, for example the position of new seeds within a growing head. There seem to be two different explanations of this growth mechanism.

The first assumes that there is a straight line on the cylinder, i.e. a helix on the surface of the stem, called the generating spiral. Buds are created along this spiral at constant time intervals and the resulting geometry creates a pattern that we interpret as the double family of spirals. This model, called the Hofmeister process, is essentially geometric in nature – there is no dynamics other than the generation process, and the Fibonacci spiral families are a consequence of the lattice created by growth on the generating spiral.

The second mechanism assumes that there is some sort of inhibitory effect due to the existing leaves or seeds, and that the new buds are generated at the least inhibited point. This leads to models based on potentials (e.g. [6]) or other maximisation principles (using distance [7] or mechanical actions [8]) or a purer geometric disc fitting [9, 10]. These models have a strong narrative that can be applied to problems in physics, an example is given in [11]. Note that some of these models are sometimes also referred to as Hofmeister processes too, in the sense that there can still be a constant time between the formation of successive buds.

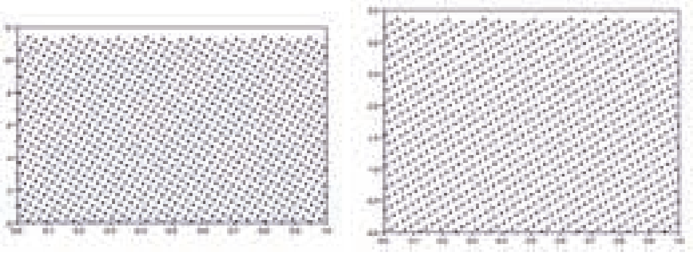

Figure 2: Bud positions for the simple generating curve model.

Probably the simplest of the geometric Hofmeister models is to assume that the process takes place on the surface of the cylinder with radius one and coordinates $(x, y) \in \mathbb{R}^2$ and with x taken modulo one in the projection onto the cylinder. The generating helix is $y = rx$ and if the buds are created at regular times they will be regularly spaced along the x direction at points dn, $n = 0, 1, 2, 3, \ldots$, and so the corresponding y values are rdn. Thus the buds are at the points $(dn \pmod 1, rdn)$. Figure 2 shows two realisations of this model. The first (left-hand) image has

$$d = \left(\sqrt{5} - 1\right)/2, \quad r = 0.013\sqrt{2}$$

so $d = g$ and r is a small number that is not rationally related to d. The resulting image has two very obvious spirals (i.e. straight lines on the cylinder): a family with fairly large positive slope (and there are 34 in the family, it being easiest to count along the top or bottom of the figure), and a family with negative slope, rather less steep than the first family, of which there are 21. Since $(21, 34)$ is a Fibonacci pair this conforms with expectations.

It could be argued that the choice of parameters, and particularly the use of the golden mean, has biased the results. So the right-hand diagram of Figure 2 shows results with

$$d = 1/\sqrt{2}, \quad r = 0.005.$$

In this case there is a large negative slope family with 41 members and a small positive slope family with 17 members. With the best will in the world, $(17, 41)$ is not a Fibonacci pair, so what is going on?

Suppose there are two families of these emergent curves (parastichy curves in the jargon of the subject) and that there are m lines in one family and n in the other. The lines are functions of two parameters, the *rise* (the parameter we called r above) and the *divergence* (d above). Let $[x]$ denote the nearest integer to x. Jean shows ([12], though Swinton [5] has recently given a more complete account) that if such a pair (m, n) exists then

$$|m[nd] - n[md]| = 1.$$

So although this model does give parastichy curves with predictable relationships, the parameters need to be tuned so as to obtain Fibonacci neighbours.

Models of the second type, those that find room for the next bud, are more compelling because there are fewer parameters to fit. One simple version of these, due effectively to Mitchison [13] models the buds as discs in the cylinder (or a cone to take time into account), so a new bud cannot come into existence until there is space for it. A typical configuration is shown in Figure 3, using a variant [9, 10] of Mitchison's conical version that uses the whole cylinder and where the numbers reflect the age of the corresponding bud, and so each bud is relabelled when a new bud enters. After a new bud is created, the whole cylinder moves forwards, leaving headroom, which increases until another bud can be placed on the cylinder. Every new cylinder (after the first few) must be tangential to at least two others. This obviously requires a more complicated geometric analysis, but Mitchison [13] and more recently Atela and Golé [9, 10] have analysed aspects of these models in some detail. The bottom line is that again they can arrange themselves in Fibonacci structures, but that there is actually greater flexibility in the cylinder model, allowing for other possibilities (e.g. whorls), which still have potential biological significance.

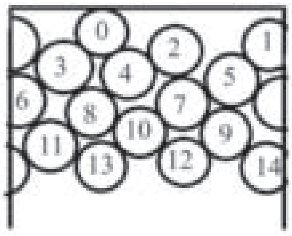

Figure 3: Schematic representation of the disc model, numbers corresponding to the age of the bud in that disc, older discs are lower down (adapted from [9]).

The phyllotaxis problem is simple to state, but even the elementary models require quite deep mathematics to analyse completely. There remains the issue of how the inhibition or activation actually happens, and the extent to which Fibonacci pairs really do arise in experiments. As part of an effort to understand this, and motivated by the centenary of Alan Turing's birth (Turing worked on simple models of the kind described here), there will be a national call to cultivation this year. The Museum of Science and Industry (MOSI) in Manchester will be coordinating a mass experiment to grow sunflowers and count the parastichy spirals. This should make both the status of statements about the appearance of the Fibonacci neighbours, and the range of other possibilities encountered, more scientific. ❏

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